

Ecology of Red Deer

A research review relevant to their management in Scotland



Institute of Terrestrial Ecology

Natural Environment Research Council



Late summer on a deer-forest in western Scotland

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Institute of Terrestrial Ecology
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Most photographs were taken by Brian Mitchell, others by Carolyn Cummins (Plate 7B), Tim Parish (Plate 1B; Plate 12, lower), Ian Paterson (Plates 1A, 6 and 7A), Brian Staines (cover, stag and browsed conifer), J.M. Sykes (Plate 8, lower), Adam Watson (Plate 11, upper) and Muriel Welch (cover, landscape).

Landscape locations are as follows: cover—Assynt, Sutherland; frontispiece—Isle of Rhum; Plates 1A and 7A—Glen Feshie, Inverness-shire; Plate 1B—Inverpolly, Wester Ross; Plate 6, lower—Glen Croe, Argyll.

1. Introduction

Complex problems of land-use associated with free-ranging populations of red deer (*Cervus elaphus* L.) in many parts of the world have stimulated a great deal of ecological research. Our objective is to assess existing knowledge relevant to the management of red deer and their range in Scotland, with a view to highlighting present research needs.

A review is opportune for several reasons. The research studies conceived over a 20-year period by staff of the former Nature Conservancy are now mostly completed, and future projects will be planned in changed circumstances. Two new bodies (Institute of Terrestrial Ecology and Nature Conservancy Council) have been created from the Nature Conservancy, and the 'customer-contractor' principle has been introduced into government research, giving greater weight to practical relevance, rather than scientific interest, as a justification of new expenditure. Also significant changes in land-use are occurring, or are likely to occur, in the Scottish uplands, with increased recreational pressures, increased afforestation, changes in forestry practice, new attitudes towards deer in plantations, and increased demand for animal protein, this being reflected in the rising value of venison and the development of deer farming.

The basic problem associated with red deer in the Scottish uplands concerns the balance between their value as a resource, and their detrimental effects on habitats and different land-use interests. As with most other resources, there is a desire to maximise output, but because deer can roam with relative freedom over large tracts of countryside, those benefiting from the resource, in terms of sport, meat production or aesthetic pleasure, do not necessarily experience the adverse effects of their presence. Farm crops and forest plantations can, however, be much damaged by grazing and browsing, and even on land specially reserved for red deer there is a need to consider the well-being of the habitat. Also it is widely believed that the performance of red deer in Scotland is relatively poor, and has been declining, because of habitat changes and over-stocking.

Our approach is to focus on those aspects of deer biology and plant ecology necessary for understanding the workings of the ecological systems of which red

deer are part. Hence deer anatomy is not considered, and morphology and physiology are only partially examined. In the fields of behaviour, performance and population dynamics, as also in vegetational dynamics, we adopt a world-wide perspective in weighing and sifting the results of research. Knowledge on other large herbivores, particularly deer species, and on the grazing process, is also taken into account.

To achieve a wildlife-management capability it is necessary to be able to predict the interactions of, and to have control over, the component parts of ecological systems; we attempt to evaluate the research findings in these respects. Whilst recognising that wildlife-management objectives generally depend on several different sorts of motivating or limiting factors, we give greater emphasis to the biological than the economic or sociological considerations.

Because of the importance of red deer to man, there is an extensive literature, with a great deal of sporting and popular material, only some of which is useful in the present context. A bibliography by Kirsch & Greer (1968) gives over 1,200 references on wapiti or American elk, and 240 on other forms of red deer, published up to December 1968; but the total of potentially relevant material is very much greater than this. We therefore mention only selected publications, and have to some extent been obliged to cite their conclusions irrespective of possible technical imperfections and debatable inferences. Techniques of investigation are discussed where these are most limiting in either research or management. Our scrutiny of the literature published since 1974 is less wide-ranging.

We have found it convenient to present first some basic information on the biology, importance and management of red deer (BM), then the literature survey in the fields of dispersion, feeding and behaviour (BWS), impact (DW), and population dynamics and performance (BM), followed by a discussion on what is known and how the gaps should be filled, together with some comments on current management. Finally, the course and achievements of the Nature Conservancy research on red deer are outlined in an appendix. All three authors are collectively responsible for the text; the initials indicate the principal writers of particular chapters.

2. Background

2.1 TAXONOMY, DISTRIBUTION AND VARIABILITY OF 'RED DEER'

The practical definition of a species from its morphological features does not always accord with the ideals of genetic discontinuity and reproductive isolation. These difficulties in taxonomy (see Huxley 1940; Mayr 1963, 1964) are well illustrated by the deer known in Europe as red deer, and those in North America and Asia known as wapiti or elk. Indeed, some authors classify red deer and wapiti as distinct species on account of their differences, but others regard them as forms of one species due to their similarities. Referring to this, Caughley (1971a) states "While the taxonomy of this group is superficially chaotic, classifications differ mainly in the taxonomic rank assigned to hierarchical levels within the complex, rather than in judgements on the general relationships between forms". Perhaps the best account is that of Flerov (1952) who accepts wapiti and red deer as forms of *Cervus elaphus*, with a total of 16 subspecies. In this review, we use 'red deer' for the whole *Cervus elaphus* species-complex, except when stated otherwise. We avoid 'elk' as, in Europe, this is sometimes applied to *Alces alces*, usually called 'moose'.

Cervus elaphus is indigenous within the 30-65° N latitude zone, with a holarctic but discontinuous distribution. Fossil and more-recent remains indicate that its former distribution was more continuous within the same latitude zone. It has been introduced in parts of the southern hemisphere, and in Australia it extends to 25°S from higher latitudes. Flerov (1952) and Caughley (1971a) give maps showing the distributions of the main forms.

Accepting wapiti and red deer as forms of *Cervus elaphus* is based mainly on morphological similarities but also, as noted by Kirsch & Greer (1968), because they have been found to hybridise both in captivity (Gray 1972) and in the wild (Flerov 1952). Caughley for example, (1971a), found intermediate forms in Fiordland, New Zealand, where red deer from Europe and wapiti from North America were introduced. Red deer and sika deer (*Cervus nippon*) have also hybridised in captivity (Gray 1972) and in various parts of the world where they have been brought together e.g. North Island, New Zealand (Davidson 1973a), Poland (Suminski 1969), Ireland (Harrington 1973, 1974), northern England (Lowe & Gardiner 1975) and perhaps in Scotland (McNally 1969). Hybridisation does not seem to occur freely; special circumstances may overcome the normal reproductive barriers. Red and sika deer in Ireland are of special interest in this respect. They have existed together for up to 100 years in several parts, with no indications of hybridisation in most. In some areas, however, there are mixed groups containing some individuals like red deer, others like sika deer, and others which appear to be intermediate.

Translocating animals within and outside their indigenous ranges for the purposes of stocking, re-stocking,

or 'improving the blood-stock' is an old tradition in game management, and its extent is inadequately documented. European red deer have been translocated more extensively than North American and Asiatic wapiti. Apart from the establishment of North American wapiti in New Zealand (Thomson 1922; Donne 1924; Wodzicki 1950, 1961; Poole 1973), a few were introduced to Scottish deer-forests (Whitehead 1960) where they apparently died out. European red deer have been introduced and established in Australia (Bentley 1957, 1967; Roff 1960), New Zealand (Thomson 1922; Donne 1924; Poole 1973), Argentina and Chile (Cresswell 1972). Moreover, the introductions to New Zealand were from several sources (Wodzicki 1950; Logan & Harris 1967; Clarke 1971). Small numbers were also introduced to Kentucky, USA (Vinson 1947). Whitehead (1964) gives extensive notes on translocations and introductions of red deer within the British Isles, but these records are known to be incomplete.

The variation of *Cervus elaphus* in size and antler form over its world range is the basis for its division into named sub-species, and at least some of this variability must be genotypic. Indeed, the North American wapiti and European red deer in New Zealand clearly differ in size, antler form, tail patch and voice, and there is at least some degree of reproductive isolation between these sympatric populations. However, red deer often differ in size between adjacent habitats, and how much of the total geographic variability is phenotypic is not known (see 5.3.1). Nevertheless, one of the reasons for moving animals from one part to another within their natural range, or from deer-parks to Scottish deer-forests, is the assumption by practical managers that big deer must produce young of high growth-potential. The genetic and ecological consequences of mixing deer from different populations and of hybridisation between species are not known.

2.2 A BRIEF BIOLOGY OF THE ANIMAL

The most-useful general accounts on the biology of red deer are those of Flerov (1952) on all forms, and Murie (1951), McCullough (1969) and Flock (1970) on those in North America. As in most other deer species, only mature males have antlers; antlerless males called 'hummels' (see Mitchell & Parish 1970) are rare and antlered females very rare. Antlers are cast in spring and regrown by late summer. The growing antlers with their soft skin are referred to as 'antlers-in-velvet'.

The new-born young (calves) and full-grown adults of red deer in Scotland are roughly twice the corresponding body weights in man, with much the same total and sexual variation. Females (hinds) are generally smaller than males (stags), the difference increasing to a maximum during adult life. Female calves (6.4kg) are c. 5% lighter in live-weight than male calves (6.7 kg) soon after birth (Mitchell 1971), whereas adult hinds (90 kg, not lactating; 78 kg, lactating) are 25-30% lighter than adult stags (120 kg) during late summer/

early autumn (Mitchell, McCowan & Nicholson 1976). In Europe, red deer increase progressively in body weight and antler size from N.W. to S.E., those in Hungary, Yugoslavia and Bulgaria having c. 2-2½ times the body weight and c. 3-4 times the antler weight of those on Scottish hill-land. Wapiti in Asia and North America are appreciably larger than red deer in Europe, the body weights being c. 3-4 times those of red deer in Scotland.

Maximum life-span is c. 20 years, and natural-mortality patterns seem to be typically mammalian with the young and the old having the highest death-rates (see 5.2.3). The animal is a seasonal breeder with single births; multiple pregnancies are rare (see 5.2.2). In Scotland the mating season (rut) is from September to November with a peak in October (Lincoln & Guinness 1973). Pregnancy extends over the winter and calving is in early summer, most calves being born from late May to late June. Lactation is prolonged and may last until shortly before the next calving season in some hinds (Mitchell *et al* 1976). Whilst the sexual cycle is governed primarily by photoperiod (Marshall 1937; Jaczewski 1954; Goss 1969a, 1969b; Fletcher 1974), other factors have secondary effects on reproduction. For example, poor condition tends to delay or prevent oestrus in hinds (Mitchell 1973a; Mitchell & Lincoln 1973; Mitchell & Brown 1974). Unmated mature hinds have oestrus cycles of c. 18 days, from around the autumn to the spring equinox (Guinness, Lincoln & Short 1971). Spermatogenesis occurs in stags throughout the period when they have 'hard' antlers, but not during the period of antler growth (Lincoln, Youngson & Short 1970; Lincoln 1971a, 1971b). Gestation is appreciably longer in Canadian wapiti (249-262 days) than in European red deer (225-245 days) (Asdell 1965). Guinness *et al* (1971) found a mean of 233 days in captive Scottish hinds.

Like many wild ruminants, red deer tend to live in groups with mature males living apart from females and young for much of the year. In Scotland, they show well-defined diurnal movements (Darling 1937; Lowe 1966), moving to lower ground at night and higher ground by day. Similarly, they occupy relatively high ground in summer, and lower ground in winter with stags usually lower than hinds.

2.3 THE STATUS OF RED DEER IN BRITAIN

Within Britain the main range of red deer is in northern Scotland, primarily in the Highlands and on some islands (Whitehead 1960) (Fig. 1). A few small relict populations and others resulting from introduction or escapes occur locally. Detailed aspects of the history, status and management of red deer in Scotland are given by Ritchie (1920), *Report of the Departmental Committee on Deer Forests* (1922), Cameron (1923), *Report of the Committee on Close Seasons for Deer in Scotland* (1954), Darling (1955), Lowe (1961), Red Deer Commission (Annual Reports 1961-1975), Royal Scottish Forestry Society (1968), Darling & Boyd (1969),

McVean & Lockie (1969), and Nicholson (1974). Only the broad features are given here, with additional material in 2.4 and the Appendix.

A population now estimated at c. 270,000 red deer occupies some 2½ million ha of hill-land in Scotland, but the main concentration is on half this area i.e. deer-forests (defined below). The animal is an important local resource, and it is sometimes argued that sport and venison production are the most effective ways of making use of the rough hill-land where red deer now live. In fact the present annual cull amounts to 25-30 thousand animals (c. 1,000 metric tonnes of dressed carcasses) i.e. a venison yield of c. 0.5 kg/ha/year. Income from venison is supplemented by sporting revenues from c. 12,000 stags killed annually in late summer by sportsmen. Hinds have no sporting value and they are killed later in the year by resident stalkers. Red deer also concern a wide section of the general public as an aesthetic feature of the Scottish Highlands.

The area where red deer occur in northern Scotland comprises over 250 private estates known as 'deer-forests', and other properties where the deer are controlled or exploited as a secondary resource. The term 'forest' in this context means a reserved hunting ground, not necessarily containing woodland. In fact the vegetation of Scottish deer-forests consists predominantly of dwarf-shrub heaths and poor-quality grasslands. Some ground is included above the zone of natural woodland which extends to around 650 m in the central Highlands; such ground has a more arctic-alpine climate and flora, and is not suitable for winter grazing, whereas lower land may be used throughout the year. Most land below 300 m has other uses, and deer are unwelcome intruders i.e. 'colonisers' or 'marauders'. However, in some parts of the north and west, deer-forests extend down to sea-level.

Red deer were indigenous throughout the British Isles at least until a thousand years ago, occurring mostly in woodland (Ritchie 1920; Whitehead 1964). It is unclear to what extent they occupied the tracts of blanket bog which had been replacing woodlands in wetter upland regions since Atlantic times. Extensive clearance of lowland woodland took place by the fifteenth and sixteenth centuries, due to agricultural demands and the needs for timber; but substantial forest areas remained in the Scottish Highlands (Pearsall 1950; Anderson 1967). Elsewhere deer were much reduced except in special 'parks' where pressures from hunting and poaching could be controlled (Whitehead 1964). Only in the Scottish Highlands had the deer an extensive habitat available, albeit largely moorland, in which they were relatively safe from over-exploitation and to which they could adapt.

Impact from man was at a peak in the Highlands in the late eighteenth and early nineteenth centuries. Woodlands were intensively utilised to provide timber (Anderson 1967), or in some areas charcoal for smelting

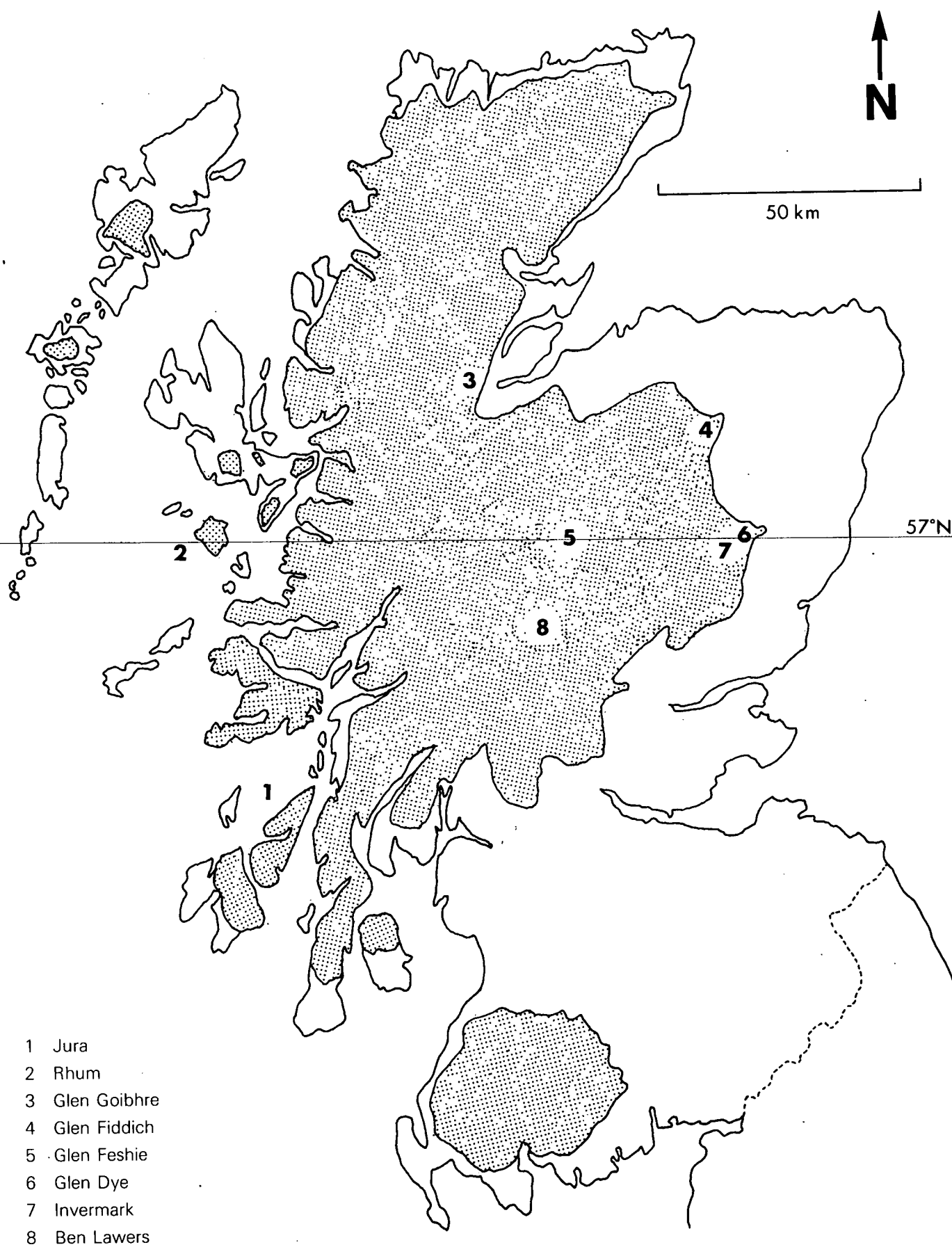


Fig. 1 Main red-deer range in Scotland (shaded areas), with study areas referred to in text.

(Lindsay 1975), and large-scale sheep farming spread into much of the region (Franklin 1952). Additional farmsteads were established, more ground was reclaimed as cultivated outfields, and shielings were sited in more-remote areas (Gaffney 1960; Miller 1967). Although singly these pressures might not have affected the habitat greatly, collectively they virtually eliminated natural woodland and increased the amount of monocotyledonous vegetation relative to dwarf-shrub heath, as attested by numerous illustrations e.g. Robson (1819), descriptive maps e.g. the surveys of Lochtayside (1769) and Assynt (1774) (McArthur 1936; Adam 1960), and accounts e.g. Robertson (1808). Only nine deer-forests were recognised in the 1790's, and the numbers of deer were much lower than at present (Cameron 1923).

In the middle years of the nineteenth century there was a sharp rise in the number of deer-forests, increasing demand for recreation by the *nouveaux riches* of industrial Britain being stimulated by the writings of Scrope (1839) and other romantics, and aided by the coming of the railways and the development of the breech-loading rifle. The profitability of sheep farming declined shortly after as imports of meat and then wool increased, and in many places sheep were removed (Hunter 1973). In the absence of natural predators, the last wolf being killed by 1750, and with shooting strictly controlled, deer numbers rose steadily. The demand for deer-stalking encouraged greater stocking rates, and little regard was given to their long-term effects. More recently pressures from afforestation, agriculture and recreation (walking, climbing) have increased, and the deer have been restricted to the poorer-quality, more remote and exposed, hill-land.

Thus, in various ways, man has modified the distribution and abundance of red deer in Britain, and in Scotland they now occupy large areas of rather atypical habitat. Here they are characterised by smaller adult size than their ancestors (Ritchie 1920; Lowe 1961) and those deer living at present in woodland habitats elsewhere in Europe. This difference is at least partly phenotypic for Scottish deer reach much the same adult size as other European red deer when reared under similar conditions (see chapter 5). Nonetheless, the possibility of some evolutionary adaptation to their atypical habitat cannot be discounted.

2.4 IMPORTANCE TO MAN

How red deer are managed in a given area depends on many factors, but the chief, usually conflicting, motivations are to control the level of damage to agricultural, forestry and other land-use interests, and to conserve the animals for sport, meat production or aesthetic purposes. The balance between these two primary motivations depends on the dominant use of the land on which the deer occur.

In Scotland, red deer are clearly the dominant interest on deer-forest land, but not on neighbouring agricul-

tural or forestry land. Thus, on Scottish deer-forests, red deer are maintained at comparatively high population densities, and management is strictly animal-oriented, contrasting with the habitat-oriented approach elsewhere. In continental Europe, red deer are maintained in commercially managed forests as a secondary resource. The need to minimise forest damage means that the deer are strictly controlled. In North America and New Zealand, the management of big-game herbivores is very much habitat-oriented, and, in the latter country, the well-being of protection forests in catchment areas which are vulnerable to soil erosion and flooding is the main concern. Red deer and various other introduced mammals have been legally classed as 'noxious animals' in New Zealand since 1952 due to their damage in such areas (Poole 1973). However, there is also much opinion in favour of treating the red deer as a resource, to be controlled and cropped as such, but not exterminated. In North America, sustained yield without habitat destruction is the principal goal underlying deer management.

Red deer are hunted for sport or for meat and other by-products throughout most of their world range. Game is state-owned with common hunting rights in North America (Taber 1965) and New Zealand (Poole 1973), but there are long traditions in Europe of legally restricted hunting rights associated with land tenure. Hunting methods vary considerably e.g. on horseback with hounds, and shooting by stalking or from fixed positions. Whereas in Scotland sporting interest centres on the difficulties of stalking and shooting stags on open land, with antlers as sporting trophies being relatively unimportant, elsewhere in Europe the hunting is more trophy-oriented. Antlers are assessed from several measurements, weight being the most important, and visiting hunters are charged accordingly. The cost is geometrically related to antler 'quality', being usually several times the carcase value of the animal. Income from leased shooting helps to pay the management costs of each hunting 'revier'. Most continental European countries have complex game laws defining the shooting seasons for stags, and hinds, and specifying which classes of deer may be taken, and in what proportions, to conserve the best for breeding.

Venison is important as the main hunting objective or as a by-product of hunting for sport. Although venison trading is illegal in North America as an anti-poaching measure, the meat is much valued by private hunters. Elsewhere, venison is a saleable product, and whereas it was mainly used for home consumption formerly, it has featured in overseas trade over the past twenty years. At present a great deal of venison is imported by West Germany. For example, over the past few years exports of red-deer carcases from Scotland amounted to c. 25,000 and from New Zealand c. 100,000 annually. Germany's total imports of red-deer venison have not apparently been published, but, in addition to those from Scotland and New Zealand, they include

c. 12,000 carcasses from Poland, 16,000 from Hungary, and some from Yugoslavia and Russia (Mitchell 1973b). New Zealand's venison exports developed over the past decade with the efforts to eliminate 'noxious animals', bounty schemes and poison baits being expensive and only partially successful. The overseas market stimulated commercial meat-hunting and deer populations began to show signs of reduction (Poole 1973). Interest in venison production led to commercial deer-farms being set up as an insurance against wild stocks being exterminated, and research projects on red-deer farming began recently at Invermay Agriculture Research Centre and Lincoln College (Rhodes 1972; Morcan 1973; Bird 1974; Wilson 1974; Drew 1976). An experimental red-deer farm was also set up in Scotland in 1970 by the Rowett Research Institute and the Hill Farming Research Organisation, following discussions initiated by the Highlands and Islands Development Board in 1969 (Bannerman & Blaxter (eds.) 1969; Blaxter, Kay, Sharman, Cunningham & Hamilton 1974). A commercial deer farm began in Fife in 1974 (*Farmers Weekly*, 29 August 1975) and another is being started by the Highlands and Islands Development Board in Argyll (*The Scotsman*, 24 February 1977).

Apart from 'offal', which has little commercial value, the main saleable products besides meat are skins, antlers and upper canine teeth. In some regions, other products have values as folk medicines and aphrodisiacs (see *Articles of Tibetan Medicine* (undated), V/O Medexport, Moscow, USSR). These include antlers-in-velvet, unborn calves, certain ligaments, tails and genitals, which are exported both from Russia and New Zealand to the Far East. Antlers-in-velvet have a much higher commercial value than the other products, and they are much easier to extract than carcasses from difficult terrain. Flerov (1952) refers to long-established traditions of farming deer in Asia for the production of antlers-in-velvet from which a folk medicine called 'pantocrin' is made.

Deer-parks have been created in most parts of the red deer's world range and some have existed for centuries (Whitehead 1950, 1960, 1969). The earliest

parks functioned more as deer-farms or private hunting preserves, but now deer are kept mainly as an attractive amenity. Some parks sell live deer for stocking or breeding purposes. In the British Isles, there are presently c. 124 deer-parks (c. 100 in England) compared with c. 334 in England alone a century ago (Whitehead 1969).

In Scotland, the value of red deer as a natural resource is clearly dependent on economic factors, as well as local traditions, aesthetic considerations and land-use requirements (Lockie 1966; Mather 1972a, 1972b; Dulverton 1975; Mutch, Lockie & Cooper 1976). For example, the future of commercial deer-farming in Scotland depends largely on the market for venison at home and abroad (Paluchowski 1976). But deer management can be influenced by many factors, some being unpredictable. Outbreaks of 'foot and mouth' disease in cattle in Europe have affected venison exports from Britain to Germany twice over the past decade. In 1968 the outbreak in England reduced the numbers of red deer shot in, and exported from, Scotland. Similarly, in 1973 an outbreak in southern Europe reduced West German imports of venison from other parts of Europe and New Zealand. Whilst 'foot and mouth' disease has never been found in red deer, the discovery of any diseases of agricultural importance (see 5.3.4) could have repercussions on their status and management. Recent West German import regulations requiring the veterinary inspection of deer carcasses have caused difficulties in the more-remote deer-forests and in those where it is possible to kill and extract only small numbers at a time. Carcasses must be cooled to 7°C within 10 hours of killing, and they must be presented unskinned along with labelled offal (heart, liver, lungs, and kidneys) for veterinary inspection at the processor's premises within 24 hours. Changes may be expected also in the demand for red-deer stalking in Scotland. There is increasing interest in roe-deer (*Capreolus capreolus*) shooting in forestry plantations by sportsmen from continental Europe, and new interest in red-deer shooting on open land and in plantations may follow. Similarly, hind shooting could develop as a sport.



Plate 1A

Central Highland deer-forest country, showing remnants of natural woodland, mainly Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.). The paler areas of vegetation are grasslands, and the darker areas are dwarf-shrub communities, mainly Callunetum; one paler patch of burned Callunetum occurs above the tree-line on the left.

Plate 1B

The rugged terrain typical of deer-forests in western Scotland. Note the presence of woodland on the ungrazed island in the loch, and its absence elsewhere. Much of the ground is clothed in blanket bog, with *Calluna* predominating on the drier hummocks, and *Molinia* in the seepage hollows.





Plate 2A

Mature stags in late March, after the snow has melted on the lower ground. The grey-brown winter coat is loose and ragged, and antler-casting will occur shortly. The summer coat is red-brown, and first becomes apparent in late May to mid June when new antler growth is well under way.

Plate 2B

Hind being suckled by ten-week-old calf in mid August. Single births are the rule in red deer, twinning being rare. Lactation ends by the following spring in most hinds.



3. Dispersion: feeding, social and other behaviour affecting distribution

Understanding dispersion, i.e. the way in which an animal occupies its range and the processes bringing this about (Wynne-Edwards 1962), is important for red-deer management in a number of ways. First, the animal's growth, fertility and life-expectation are affected by where it chooses, or is obliged, to live. Secondly, its dispersion brings it into contact with man's interests; deer may be welcome as an asset or resource in some areas but unwelcome as a cause of damage in others. Finally, the area an animal occupies does not necessarily reflect its optimum preferences or requirements, but is usually the result of the interactions between the animal's behaviour and the limiting environmental factors.

3.1 FACTORS AFFECTING GROSS DISTRIBUTION
Red deer are always associated with woodland habitats in continental Europe (Table 1). Ahlén (1965a) suggests that areas of 1,000-2,000 ha of woodland are needed for permanent occupation by red deer in Scandinavia, and in Hungary and Poland it is accepted that there must be at least 1,000 ha to support a permanent red-deer population (Mitchell 1973b). Red deer are found in purely deciduous forests (Yanushko 1957;

Meyer 1972), mixed coniferous-deciduous (Rusanov 1963) and pure coniferous forests or plantations (Zai 1964; Baskin 1965).
In North America, all the existing sub-species with the exception of the Tule elk (*C. elaphus nannodes*) are also found associated with woodland or woodland scrub (see Murie 1951 for general review; Dalke, Beeman, Kindel, Robel & Williams 1965; Harper, Harn, Bentley & Yocum 1967; Boyd 1970; Knight 1970; Craighead, Attwell & O'Gara 1972). They are generally found in mountainous regions, but occur also in lowland forests e.g. *C. elaphus roosevelti* (Murie 1951). Murie is inconclusive about the distribution of wapiti before man had a marked effect through over-hunting, but concludes that they were always present in mountainous country and their presence there today is not secondary due to harassment by man. It is likely that they always occurred on the plains but the extent to which this was a seasonal or widespread occurrence is not clear. The Tule elk, however, is primarily an animal of open grassland (McCullough 1969), and did not apparently occupy the chaparral or woodlands on the adjacent mountain slopes (Murie 1951). Of the various sub-species it appears to have the greatest tolerance to arid conditions.

Table 1. Habitat types occupied by red deer in Europe and North Africa

HABITAT TYPE					
Country/Area	MOUNTAINOUS/HILLY		FLAT GROUND		Authors
	Woodland	Non-woodland	Woodland	Non-woodland	
Bavaria	+				Mitchell 1973b
Czechoslovakia	+				Bališ.1965
Denmark			+		Jensen 1968
Eire		+			Whitehead 1964
England (E. Anglia)			+		" "
" (South-west)	+	+	+		" "
" (North-west)	+	+			" "
Holland			+		Eygenraam 1959
North Africa	+				Salez 1959; Meyer 1972
Norway	+				Wegge 1974
" (Aure)			+		" "
Poland			+		Dzięciotowski 1969
Sardinia	+				Jenkins 1972
Scotland	+	+	+		Own data
Sweden	+		+		Ahlén 1965a
Switzerland	+				Gossow 1974
U.S.S.R.	+		+		Flerov 1952; Samoilov 1962; Rusanov 1963; Sablina 1969
Yugoslavia	+				Valentinčić 1960; Bojović 1967
" (Belje)			+		Bojović 1967; Brna <i>et al</i> 1970

A common feature of the woodland habitats where red deer occur is the presence of grassy clearings, fields, forest-rides etc., within, or adjacent to, the woods (Samoilov 1962; Dzięciołowski 1969); they rarely occupy large, dense forests. Flerov (1952) states that "they undoubtedly originated in the forest steppe zones or sparse forests. It may be precisely for this reason that deer remain close to the forest-steppe slopes, with meadows covered by grass. More rarely they enter sloping rocky forest regions, but they are completely absent in the naked rocks and stretches of stones. Deer are also absent among unbroken forest complexes". He also states that they were once animals of the plains and that "affinity to mountains represents a secondary phenomena caused by displacement from the valleys by man" (see also p 9, and Murie (1951) for similar evidence on North American wapiti). Likewise, Dzięciołowski (1969) concludes that red deer are "inhabitants of a borderline between forest and steppe formation".

The association with the woodland edge, or the interface between woodland and grassland, is also found in areas where red deer have been introduced. In Queensland, they are found in largest numbers where cleared grassy slopes, open forest and rain forest are in close proximity (Roff 1960), and in New Zealand, where "forest, scrub, grassland or open mountain top lie close together" (Wodzicki 1961, 1963; Howard 1966; Clarke 1971). Even on the flat pumice areas of North Island (e.g. Kaingoroa) the association is with forest and forest edge (Wodzicki 1961; Mitchell 1973b). In New Zealand, red deer colonised the indigenous beech forest (*Nothofagus* spp.) more easily than the hardwood/mixed podocarp forest and occur also in exotic coniferous plantations (Wodzicki 1961; Howard 1966).

In the British Isles, however, the greatest concentrations of deer are found in the treeless areas of the Scottish Highlands (Table 1). In Eire (e.g. Wicklow) and S.W. England (e.g. Exmoor), they may also live entirely on open-hill ground, although in the latter area some deer only use forested areas (Lloyd 1971). There is little doubt that living permanently on open-hill land is a recent phenomenon and that formerly the animal was a woodland/woodland-edge species in Britain, but from Neolithic times there has been an increase in the open ground/forest ratio (2.3). In other parts of Great Britain the larger concentrations of deer still conform to the general pattern; thus in Furness (N.W. England) they occur in woodland on hillsides, and in East Anglia and the New Forest in woodland on flat ground. Deer are also found in coniferous plantations and other woodlands in Scotland; but they may use forests only in bad weather if open-hill ground is available nearby (Sobieski & Stuart Vol. 2 1848; Darling 1937; own observations). The reasons for these differences are not clear, for there are no objective studies of the effects of woodland structure on deer behaviour nor of the differences in behaviour between deer on moorland and in forests.

The question remains, however, how deer exist on open moorland in Britain, when, elsewhere, woodland appears to be an 'essential' part of their habitat. Open hill-land in Britain may give the deer the same essential habitat features as woodland. Browse, mainly in the form of heather (*Calluna vulgaris*), is available, as is other suitable forage (e.g. grasses, sedges). Also, they get shelter by using topographic features, and select places on hillsides where they have an unrestricted view (see also 3.2.4.2), which may compensate for the 'sense of security' given by woodland cover. That they do not continually inhabit flat land without forests suggests that 'cover' is a very important requisite for the permanent occupancy of an area by red deer. In contrast, other species normally found in woodland, such as roe deer, do occupy such ground (Geist 1974; Kafuziński 1974).

The northern limit of red deer in Europe and Asia does not appear to coincide with the plains or hilly ground, nor with the forested zone (Flerov 1952). It is generally thought to be set by snowfall (Formozov 1946; Flerov 1952; Nasimovich 1955; Sablina 1969), and, according to Formozov, red deer do not occur further north than where the average yearly maximum snow depth is 40-50 cm (we assume that this is on level ground and does not take into account local drifting). They are only found in large numbers where snowcover does not exceed 20-30 cms. At the northern edge of their range in Norway, deer are concentrated into small areas in winter because of heavy snowfall (Wegge 1974). However, apart from Formozov (1946) and Nasimovich (1955), there are few detailed studies on the effects of snow-type, hardness etc. on red deer as, for example, with caribou (*Rangifer tarandus*) (Pruitt 1959). In Britain, deer are found up to the northern seaboard, and snowfall is important only in restricting local ranges within the country.

The responses of deer to climatic factors other than snow have been little studied, and the literature on this subject contains mainly anecdotal or circumstantial evidence. However, moisture and temperature are likely to be important in limiting world distribution, particularly at lower latitudes. Red deer are not found on many steppe areas (Flerov 1952; Samoilov 1962), where rainfall is generally low, and drinking places are important to deer in summer in some parts (see Flerov 1952; Mambetzhumayev 1961; Sablina 1969). Meyer (1972) found that Atlas deer (*C. elaphus barbarus*) moved into areas with more-permanent water supplies during dry periods and also changed from feeding on forbs and grasses to shoots and leaves. Knight (1970) similarly gives evidence of a change in habitat-use and feeding ecology in *C. elaphus nelsoni*; when water became limiting, the deer changed from a forb to a grass diet. Jenkins (1972) hints at similar limitations being likely for *C. elaphus corsicanus* in Sardinia. The high humidity in woodlands may account for deer being found in some areas of eastern Europe with an apparently low precipitation.

Red-deer distribution is also affected by mountain ranges e.g. Urals, Himalayas, Italian Alps, Pyrenees, deserts e.g. Gobi, and altitude (Wodzicki 1961; Clarke 1971). Large blocks of high mountainous country, forests or thick bush are unsuitable, and are as much a barrier to red-deer movements as are plains, steppes and deserts (Flerov 1952). Gibb & Flux (1973) found little evidence of deer movement between the upper and lower edges of some dense forests in New Zealand, and Flerov (1952) and Dzięciołowski (1969) state that red deer were never abundant in large, dense, unbroken woodland complexes.

Within the limits set by climate and gross habitat features, man is probably the next most important factor affecting the gross distribution of red deer. The range of some North American sub-species has been reduced through harassment and hunting, and some populations and sub-species have been exterminated (Murie 1951; McCullough 1969; Boyd 1970). A similar suggestion is made for red deer in continental Europe and Asia (Flerov 1952). Red deer became extinct in the lowlands of Scotland in the 17th century (Ritchie 1920) and were also greatly reduced in number in England by this time, because of hunting and the destruction of their forest habitats. Even today, red deer do not occur in many areas of apparently suitable habitat adjacent to their range, and it seems likely that human occupation or pressure is responsible for this. However, man also creates new suitable habitat, such as forestry plantations.

3.2 FACTORS AFFECTING LOCAL DISTRIBUTION

Knowledge on the factors influencing the grosser distribution of red deer is important in the long-term planning of land use for large areas, but a different set of environmental factors affect dispersion at the local level. These factors are now treated in turn; an understanding of their effects is needed for management in Scotland, which takes place within relatively small units.

3.2.1 Food and nutrition

3.2.1.1 Nutritional requirements. The performance of red deer is generally lower in Scotland than in most other parts of their range (see 5.2). They live on exposed hill-land, generally with poor soils overlying acid rocks, and, whatever the factors limiting them to such areas, the proximal one affecting performance is likely to be inadequate nutrition. In order to manipulate populations for any management system, or to create new systems, we need to understand the nutritional requirements of deer and how these will be met in different environments. We need to be able to predict the performance of animals at different densities in given areas and how this relates to the potential of an area for production. We also need to know the nutritional requirements of deer in order to understand plant selection or to predict usage.

The digestive physiology and nutritional requirements of domestic ruminants are well documented (e.g. Blaxter 1962; McDonald, Edwards & Greenhalgh 1969; Church 1969; Church (ed.) 1971, 1972), and Verme & Ullrey (1972) and Gasaway & Coady (1974) have recently reviewed feeding and nutrition in deer species. Most work on deer nutrition has been done with *Odocoileus* spp., and the principles and generalities discussed here are mostly derived from these studies, since there is less information on red deer.

The requirements of deer vary with age, breeding condition and season. Wild deer show seasonal trends in voluntary food intake (VFI) which are presumably relevant to their requirements. For example, VFI in winter is lower than in summer when there are demands for growth, lactation and storing fat for the rut and for winter. Both wild and captive deer show this reduction in VFI in winter, even when adequate food is available (e.g. McEwen, French, Magruder, Swift & Ingram 1957; Long, Cowan, Strawn, Wetzel & Miller 1965; Nordan, Cowan & Wood 1968; Short 1969; Drodzdz & Oziecki 1973; Blaxter *et al* 1974; Pollock 1974), and it has been shown, experimentally, to be associated with decreasing day-length (Simpson 1976). The reduction in VFI is more noticeable when the animals are on a high plane of nutrition all year round, and it may have evolved as an adaptation to meet winter food scarcity (McEwen *et al* 1957). Since food intake is partially regulated by the passage of food through the gut (Gasaway & Coady 1974), reduced VFI in winter is also, no doubt, partly due to the lower digestibility of winter forage, and to increased retention time in the rumen. Other major changes in VFI occur during the rut, when in males it can be considerably reduced e.g. c.50% (French *et al* 1956), and to 27% by weight of the higher pre-rut levels (Cowan, Wood & Kitts 1957). Male black-tailed deer (*O. hemionus*) can lose up to 35% of their body weight (Nordan *et al* 1968) and red-deer stags 11% (Table 9, 5.2.1). Females also show a reduction in VFI at this time, although this is not so marked as in males.

The most important nutritional factors likely to be limiting red-deer performance in Scotland are metabolisable energy, protein, and possibly calcium and phosphorus. Of these, metabolisable energy is likely to be the most common limiting factor, although protein may also be low in some areas affecting the utilisation of energy (Hobson, Mann, Summers & Staines 1976).

Many authors have related growth and performance to diets with different amounts of crude protein (e.g. French, McEwen, Magruder, Ingram & Swift 1956; Verme 1963, 1967; Murphy & Coates 1966; Ullrey, Youatt, Johnson, Fay & Bradley 1967; Robinette, Baer, Pillmore & Knittle 1973). It is generally accepted that deer need 6-7% crude protein for maintenance, but at least 13-20% for optimal growth (% dry matter).

Daily maintenance requirements for red deer have been calculated by Arman (1974) as 1,450-1,850 g dry

to feed on grasslands at lower elevations (Darling 1937), although this daily movement was reversed in a herd managed under intensive farming conditions (Blaxter *et al* 1974). On the other hand, Yanushko (1957) and Mambetzhumaev (1961) state that deer are active during both day and night, except in summer when they remain at rest during hot periods.

In more-detailed studies on activity, mainly on captive red deer, Bubenik & Časnocha (1965), Bubenik & Bubenikova (1967), Lochman (1967) and Bützler (1974), described red deer as polyphasic, having between 6-9 feeding cycles per day. Since two-thirds of the feeding periods occurred during daylight (see also Craighead, Craighead, Ruff & O'Gara 1973) these authors all regarded red deer as basically diurnal. Bubenik & Bubenikova (1967) also suggest, from experiments on a few individuals, that differences in activity can occur according to the physiological state of the individual. They found that nursing hinds had feeding cycles similar to their calves but different from non-nursing hinds, and Jackes (1973) referred to possible differences in daytime activity between stags and hinds in north Scotland. Craighead *et al* (1973) found large variation between individuals in *C. elaphus nelsoni* in the same area when other factors such as disturbance and weather were similar, but that they tended to "conform to herd patterns". Differences in grazing activity due to weather are also suggested (Darling 1937; Bubenik & Bubenikova 1967; Harper *et al* 1967) Kuznetsov & Dmitriev 1970), and disturbance such as hunting can be important, so that animals alter their feeding activity and remain in cover during the day (e.g. Darling 1937; Ahlén 1965a; Davidson 1973b; Jungius 1974) (see also 3.2.3.). The structure of the habitat may be important also since Andersen (1961) found that roe deer on heathland in Denmark fed at intervals during the day, but when transferred to woodland they became morning and evening feeders after only 3 months. Bubenik & Časnocha (1965) suggested that high-quality concentrated food put out for deer in winter upsets their normal pattern of activity.

It is difficult from these studies, therefore, to infer the 'normal' pattern of feeding activity, and the extent to which this is distorted by environmental factors. However in Czechoslovakia (Bubenik & Bubenikova 1967; Lochman 1967), synchrony of feeding cycles was related to daylight. One might expect, therefore, that deer in more northerly latitudes where day-length is shorter in winter would have a different feeding regime.

To understand the consequences of such feeding cycles, we need some measure of intensity of grazing or forage intake on the different vegetation types, not merely the time spent on each (see Rawes & Welch 1969), for communities may differ in quality. Also an animal has to work harder on closely-grazed swards for comparable amounts of food than with say a dwarf shrub like *Calluna*. The intensity of grazing on different communities is not known for Scottish red deer, but studies directed at the daily feeding-cycle would be use-

ful and could also highlight the importance of the other environmental factors which affect feeding activity. There is a lack of information on nocturnal activity in wild red deer in Scotland and, since the hours of darkness may be two-thirds of the day-length in winter, this is a serious omission. Colquhoun (1971) tried to study nocturnal activity in red deer, but was limited to observations on moonlit nights. Craighead *et al* (1973) got over difficulties of observing *C. elaphus nelsoni* by using motion-sensing transmitters.

3.2.1.3 Species eaten. Red deer eat a wide variety of species. The plants eaten vary according to habitat type and geographic and climatic zones. We can summarise the existing data to interpret general feeding habits, although it is unwise to extrapolate too far.

The main methods involved in studies of plants eaten by deer have been reviewed by Short (1966), Dzięciołowski (1967a), Hofmeyr (1970) and Jackson (1974). These are: (1) identifying plant particles in the rumen and (2) in the faeces; (3) direct or indirect (e.g. tracking) observations of wild or captive animals; and (4) examination of feeding areas i.e. utilisation studies. Probably the most common methods employed on red deer are the first (e.g. Eygenraam 1959; Jensen 1968; Dzięciołowski 1970a; Staines 1970) and third of these (e.g. Ahlén 1965a; Harper *et al* 1967; Dzięciołowski 1967b; Knight 1970; Colquhoun 1971; Charles, McCowan & East 1977). Faecal analysis has been less used with red deer (e.g. Hegg 1961; Danon, Blaženčić & Bogović 1967; Colquhoun 1971; Batcheler & Christie — unpubl., quoted in Gibb & Flux 1973, p 355; Charles *et al* in prep.), as have studies involving the examination of feeding areas (e.g. Ahlén 1965a; Miller 1971). No one method is completely satisfactory (Table 3) and ideally two or more should be used in conjunction (Dzięciołowski 1967a, 1969; Colquhoun 1971; Charles *et al* 1977 and in prep.).

There is a lack of studies justifying many field techniques. Rumen analysis is still widely used although Norris (1943) and Bergerud & Russell (1964) pointed out its dangers for sheep and caribou respectively. Few experiments have related rumen and faecal analyses to intake in red deer (cf. Charles *et al* 1977; Staines 1970, 1976a), although this has been done on other animals (e.g. Hercus 1960; Storr 1961; Stewart 1967). Considering the potential value of this latter method, and the relative ease of experimentation, this seems a serious omission.

There are considerable differences in the number and range of species eaten by red deer. Kufeld (1973) recently reviewed 48 feeding studies of *C.e. nelsoni* and found a total of 159 forbs, 59 grasses and 95 shrubs to be eaten. Egorov (1967) listed 66 species of grasses, shrubs, trees and forbs together with lumped categories for mushrooms, lichens and mosses eaten by red deer in Yakutia (northern USSR). Yanushko (1957), likewise,

listed 27 species of trees and shrubs and 81 of 'grassy vegetation' (translation) in the Crimea, and Dzięciołowski (1970a) 49 in Poland. Fig. 2 summarises the results of several studies, and it can be seen that large differences occur in the amounts of the major plant groups eaten between areas.

Few studies of feeding ecology in red deer in the British Isles have been concerned with this alone, most being by-products of other studies (cf. Charles *et al* 1977 and in prep.). Most are, as yet, in the form of unpublished theses or are still in progress (Table 4). There is little work that helps us understand food selection at a detailed level, either in relation to the quality of plant species, or to the actual mechanisms of selection. The studies are useful in that they show differences in the groups of plants eaten, the time spent on different plant communities throughout the year, or feeding differences between types of animal within a study area. Care is needed in comparing the results of studies made in different areas where the techniques used, the communities available and other environmental variables may be dissimilar. It is clear that dwarf shrubs, mainly *Calluna*, are a very important food, at least in terms of quantity taken (Fig. 2). Forbs do not form such an important part of the diet in Scotland as they do elsewhere, probably because they constitute a low proportion of the available forage.

3.2.1.4 Factors affecting plant selection Selection is not just a matter of one species being preferred more than another, but may depend partly on what else is on

offer. Mule deer (*O. hemionus*) may eat relatively small proportions of *Artemesia tridentata* when it is fed alone, but large amounts if other, highly preferred species are also available (Dietz, Udall & Yeager 1962; see also Leopold, Riney, McCain & Tevis 1951; Klein 1970; Dasmann 1971). Heather, the main dwarf shrub in the European studies quoted in Fig. 2, is taken in different amounts according to area apparently irrespective of the amount on offer, and this may relate to site characteristics (geology, soils, climate), or the presence of other more or less palatable food species. For instance, Staines (1970) found heavier browsing by red deer on heather when it was in association with blaeberry (*Vaccinium myrtillus*) and *Deschampsia flexuosa* than when it was in a pure Callunetum. Kossak (1976) has developed this theme further, and suggests that deer prefer "food blocks", rather than particular species, and that a pair of species can complement each other in the diet. Selection for a single plant species may also vary between individual animals (e.g. Rijcken 1965; Jensen 1968) or between years (Ahlén 1965a) in the same area. Both these aspects were apparent in the utilisation of young growing shoots of *Eriophorum vaginatum* by red deer in north-east Scotland (Staines 1970).

3.2.1.4.1 Extent of selection: Ruminants can be highly selective in their choice of foods. In general, they select leaf in preference to stem, and green material in preference to dead (Arnold 1964a). They can also select certain species within a mixed sward even though that

Table 3. Some limitations of different methods used to estimate forage selection and intake by free-ranging deer

Method	Limitations
Identification of plant material in rumen samples	<ol style="list-style-type: none"> 1. Plants break down at different rates into unidentifiable fragments by mastication, rumination and digestion. 2. Differential digestion of different species. 3. Different rates of passage of particles from the rumen/reticulum. 4. Animals feeding on different plants at different times of day. 5. Relates mainly to food of the previous 48 hours. 6. Non-repeatability of samples — animals generally killed.
Identification of plant material in faecal samples	<ol style="list-style-type: none"> 1. The cuticle of some species is completely digested. 2. Differential digestion of the cuticle in different species. 3. Rates of passage through the gut may differ between plant species. 4. Not always possible to decide which species or type of animal produced the droppings.
Direct observations on the distribution and activities of the animals	<ol style="list-style-type: none"> 1. Often cannot estimate amounts of different species or plant parts taken. 2. Cannot differentiate species or plant parts taken — only communities grazed. 3. Less easy to make detailed observations at night or in woodlands.
Indirect observations on animals from animal tracks or products	<ol style="list-style-type: none"> 1. Some observations are restricted to certain weather conditions e.g. tracks in snow. 2. Cannot tell which class of animal did the browsing/grazing and sometimes on which plant species.
Measurements of losses of plant material due to grazing	<ol style="list-style-type: none"> 1. Cannot tell which type or animal species grazed when several are present. 2. Exclosures to estimate herbage utilisation are not reliable since grazed plants perform differently to ungrazed ones.

species is in relatively low proportions. Similarly, they can select richer areas of any particular sward (Swift 1948) or even individual plants which are higher in nutrients (Smith 1950). Welch (1971a) found that utilisation by red deer over a twelve-month period was 67% greater on *Agrost-Festucetum* given lime and phosphate than on a similar and immediately adjacent sward. Holloway (1967) showed that red deer browsed more heavily on replanted nursery-grown seedlings of Scots pine (*Pinus sylvestris*) than on naturally-regenerating ones and browsing severity increased after fertilising seedlings, particularly with nitrate. Also, in North America, the percentage utilisation of browse species was increased after applying nitrogen fertiliser (Bayoumi & Smith 1976).

Burning may also affect the degree of utilisation of an area and many herbivores prefer to feed on the subsequent growth because it is more accessible and more nutritious (Miller & Watson 1974). Miles (1971) found that the grazing intensity of red deer on *Molinia* grassland increased sharply in the spring and summer immediately after burning, but no one seems to have confirmed the widely-held belief that deer make greater use of newly burned *Callunetum*. However this is implicit in their observed responses to the introduction and cessation of burning on the Hebridean islands of Jura and Rhum (Evans 1890; Lowe 1969, 1971). Both

workers associated higher deer fecundity with regular muir-burn, and Evans also believed that deer mortality was reduced, so that six years after burning began the hind population had risen by 50%.

3.2.1.4.2 Plant habit: The form or habit of a plant may also directly affect its use by an animal. Thus in heavily-browsed forests much of the current-year's growth may be out of reach, and other species may be unavailable because of their position e.g. on cliff ledges, or the accumulation of dead litter above the growing shoots, or because of animal-repellent characteristics (barbs, thorns, noxious chemicals etc.). It is also likely that preferred species will be selected only when they are present above a certain critical percentage in the sward. If their density is too low or they are too widely dispersed, then it may not be worth the animal's while to seek them out.

3.2.1.4.3 Food quality: Plant species may be selected for different reasons. Some may be selected on the basis of their mineral content, others because of protein, energy value or roughage (e.g. see Juon 1963). Ruminants seem to have the general ability to select a 'balanced diet' (Lockie 1967) but as Arnold (1964b) points out "No single chemical constituent has been found to determine the acceptability when a large number of herbage species are on offer". The main factors affecting

Table 4. Studies involved with red-deer feeding in the British Isles

Authors	Objectives of main study	Techniques used
Blaxter <i>et al</i> 1974	Investigation into farming red deer as a meat resource.	General observations. Observations following two tame hinds during the day and night, measured as no. of bites. Summer only.
Charles, McCowan & East 1977 and in prep.	Relating food availability to selection and movements of deer, describing what foods deer eat throughout the year and measuring seasonal changes in the grazings that may affect their nutritional status and availability.	Direct observations throughout the day. Faecal analysis of diet. Usage by density of faecal material and measures of grazing and plant growth.
Clutton-Brock & Guinness in progress	Evolutionary aspects of social behaviour in red deer including examination of the environmental and behavioural factors affecting dispersion.	Direct observations on known individuals — spot and continuous observations of communities grazed.
Colquhoun 1971	Describing and comparing the grazing ecology of red deer and Blackface sheep to assess the likelihood or otherwise of competition between them.	Direct observations. Faecal analysis for diet.
Hobson, Mann, Summers & Staines 1976	Extended test of a small mobile laboratory under field conditions and to contribute to the understanding of the rumen digestive-processes in hill sheep, red deer and reindeer.	Rumen analyses — method as Staines (1970) below.
Holloway 1967	Investigating damage caused by red deer and other animals on Scots pine, and the effects on natural regeneration.	Observations of browse spp. (i.e. assessment of what is taken from the plants themselves). Rumen analyses, air-dried weight.
Jackes 1973	Describing patterns of habitat use by stags and hinds.	Spot observations of communities being grazed.
Staines 1970, 1976a	Factors affecting the seasonal dispersion of a marauding red-deer population and its population dynamics. Experiments on rumen-cannulated deer to relate the amounts of heather in the diet with those in the ruminants.	Spot observations on communities used and rumen analyses — % no. particles from an adapted line-intercept technique; currently being adapted to % volume.
Staines, Crisp & Parish in prep.	Factors affecting the segregation of stags and hinds. Comparison of food quality between stags and hinds.	Rumen analyses — % volume

the nutritive value of a plant for an animal are (1) stage of maturity (Cook & Harris 1950), (2) soil factors, (3) climate (Short 1969), (4) variations within the plants (toxins, rate of growth etc.) (Nagy, Steinhof & Ward 1964) and (5) the condition of the vegetation (e.g. related to previous land management or animal use altering plant successions) (Taber & Dasmann 1958).

The main ways of assessing forage quality in ruminants are:

- (i) Using chemical analyses of the main food species as indices (e.g. Dietz *et al* 1962; Brüggemann, Giesecke & Walser-Kärst 1968; Dzięciołowski 1969).
- (ii) Feeding natural feedstuffs to captive animals, measuring *in vivo* digestibilities and relating to animal performance (e.g. Brüggemann *et al* 1968; Ullrey, Youatt, Johnson, Fay, Brent & Kemp 1968; Staines 1969).
- (iii) Making estimates from wild deer; e.g. *in vitro* digestibility studies (Hobson *et al* 1976), chemical indicators in the faeces (Church 1969, vol. 1, chapter 8) or the chemical composition of rumen contents (Bissell 1959; Klein 1962; Klein & Schønheyder 1970; Staines & Crisp *in press*).

None of these methods is unbiased, so that, ideally, one should always be used in conjunction with another. They do however, provide indices of food 'quality', although there is not much experimental evidence supporting the use of the techniques for red deer cf. *Odocoileus* spp. (see Klein 1970; Dasmann 1971 for reviews). It is reasonably assumed, from little direct evidence, that red deer have the capability to select for quality, but to what extent is unknown. It could be dangerous to extrapolate from smaller species to larger ones since the former can be more selective in their choice of plant material (Jarman 1974).

Preferred plant species are usually high in nitrogen, phosphate and gross energy but low in fibre, cellulose and essential oils (see Arnold 1964b; Heady 1964). However, some plant species high in crude protein may not be preferred because of the presence of essential oils which have an inhibitory effect on the rumen micro-flora (Nagy, Steinhof & Ward 1964; Oh, Jones & Longhurst 1968). Juon (1963) and Klötzli (1965) suggested that tannins present in some species may act as an attractant through taste, but this was discounted by Prins (1968). Heady (1964) stated that tannins are believed to decrease forage preference in domestic stock, although tannic acid positively influenced preference for hay in cattle (Hawkins 1955). From work on Scottish Blackface sheep, Milne (1974) suggested that tannins present in heather may protect some of the protein from microbial and enzymic digestion. Thus, in naturally occurring plant species which may have relatively large

amounts of essential oils or tannins, the estimation of food quality by field techniques using faecal and rumen analyses needs further investigation, otherwise erroneous conclusions could be drawn.

In fact, Longhurst, Oh, Jones & Kepner (1968) suggest that plants may be avoided because of their unpalatability which the animal learns by association with the presence of different aromatic substances. They also suggest that deer first select on the basis of smell followed by taste. Detailed studies on the senses used in food selection similar to those done on sheep (Arnold 1966a, 1966b) have not been made on red deer.

Few investigations have been made on the value of different forages for red deer in the British Isles. It is generally accepted that what is good for hill sheep will be good for red deer, but with little supporting evidence. Maloiy & Kay (1971) fed red deer and sheep similar experimental rations and concluded that the digestive processes of the two species were essentially similar, although small differences did occur. The apparent digestibility of dry matter was slightly less in deer as Simpson (1976) and Arman, Kay, Goodall & Simpson (*in prep.*) also found. Works on the nutritive value of upland plant species to sheep include Armstrong & Thomas (1953), Black (1967), Milne & Bagley (1976), Smith & Thomas (1956), Thomas (1935a, 1935b, 1936, 1937, 1955, 1956), Thomas & Armstrong (1952), Thomas & Dougall (1939), Thomas & Fairbairn (1956, 1957), Thomas & Smith (1954) and Thomas & Trinder (1947).

Staines (1969) found that the apparent digestibility of heather by red deer (41%-42%) was much lower than it was for dried grass (64%-67%), but since the animals were in negative nitrogen-balance, he assumed that deer in the wild were better able to select more-nutritious food than that forced on them by the experiment. Milne, MacRae, Spence & Wilson (1976) give similar estimates of dry matter digestibility of heather by red deer (45%) which, in their experiments, was similar to that by Blackface sheep, but the dry matter digestibility of an *Agrostis-Festuca* mix was lower, being 40%-42% compared with 48%-49% in sheep. Hobson *et al* (1976) used *in vitro* techniques to compare the digestive processes of hill sheep, red deer and reindeer (*Rangifer tarandus*) in the field. Red deer were able to ferment heather better than grass all year round, even though the proportions of the different herbage eaten changed with season. Fermentation rates in sheep were generally lower, but this may have been due in part to sampling biases. Compared with hill sheep, red deer have higher maintenance requirements per unit of body weight (Simpson 1976). Higher requirements together with lower digestibility of some forages would thus mean that deer need a greater food intake. In fact, Arman *et al* (*in prep.*) have shown that food intake is about 30% higher in red deer than in sheep per unit of body weight.

In comparisons of food quality between stags and

hinds in two different areas of Scotland (Staines & Crisp in press; Staines, Crisp & Parish in prep.), Klein's (1962) technique of estimating forage quality from the chemical analyses of rumen material has been used. Despite its biases, this technique is valid for within-area comparisons provided that there are no inter-sex differences in the ability to digest natural foods (Hobson *et al* 1976). As one might expect, the seasonal pattern of rumen nitrogen is similar to that of the vegetation (see also Staines 1970) and hinds had higher concentrations of rumen nitrogen than stags for most of the year (see 3.2.4.4).

Another important aspect on which we have little information is the relative effect of food quality throughout the year on performance. It is often assumed that winter range is limiting for red deer in Scotland, but hinds are dependent on summer-range quality for lactation and later for fertility (Arman, Kay, Goodall & Sharman 1974). The calf, in turn, initially depends on the mother's milk, and later, on the summer and autumn vegetation for growth and condition; those in better condition before the winter are more likely to survive. Recent work by Arman (in prep.) shows that the growth rates of captive calves that were suckled on well-fed hinds were 273-417 g/day over the first 30 days. Growth rates were comparable with those of wild calves up to about 120 days but, after this, wild calves had a reduced growth rate which she attributed to the decline in food quality in autumn. Hence, she suggests that summer-range quality does not limit milk production, although body condition and subsequent fertility of the hinds may be affected. (see 5.2.2).

Work on many important aspects of red-deer feeding ecology in the British Isles is lacking. There is little information on the relative qualities of different foods on red-deer range, or of the factors affecting animal selection of these foods. Such work is necessary if we are to construct predictive models for red-deer management as used, for example, on the continent of Europe (e.g. Bubenik 1959; Ueckermann 1960).

3.2.2 Weather

Apart from the effect on activity already discussed (3.2.1.2), weather affects the animals directly through their energy metabolism (i.e. heat loss or heat stress, Moen 1973) and thus evokes shelter-seeking behaviour. By seeking shelter, deer may not be able to forage so widely or feed on the plant communities which they prefer. Also, they may have to use more energy through feeding during bad weather. Snow impedes movements and covers up their food supply. Weather also affects deer indirectly through the quantity and quality of their food.

3.2.2.1 *The effect of weather on energy metabolism.*

An animal loses heat by radiation, convection, conduction (sensible heat-loss) or by evaporation (evaporative heat-loss) (Blaxter 1962). Although red deer in hotter

climates will be exposed to considerable heat-stress in summer (Mambetzhumaev 1961; McCullough 1969; Meyer 1972), in the British Isles cold and chilling conditions are probably the most important weather factors. In summer, when energy requirements are high for growth and lactation, food quality is also relatively high, but in winter, food quality is lower, animals lose weight, are in negative energy-balance and use up fat reserves. Low air temperatures affect fermentation rates in the rumen through decreased microbial populations (Hobson *et al* 1976) and food utilisation is lower (Armstrong, Blaxter, Graham & Wainman 1959). Gerstell (1937) found that, below 37° F, white-tailed deer lost heat rapidly irrespective of food supply. Brockway & Maloiy (1968) made limited experiments with calorimetry and suggested that red deer lose more heat than black-faced sheep at equivalent temperatures. This has been subsequently confirmed by Simpson (1976), who also suggests that deer may be less well insulated than hill sheep. These experiments were done in still air and heat-loss from animals increases with wind speed (Blaxter, Joyce & Wainman 1963; Moen 1973).

3.2.2.2 *Shelter-seeking behaviour.* The animal has little control on its sensible heat-loss which is determined by the "physical attributes of the environment" (Blaxter 1962). In free-ranging animals this may be minimised by their shelter-seeking behaviour. Red deer are particularly mobile animals and can seek shelter over a wider area than less-mobile domestic stock. The value of good shelter and cover is emphasised in many studies (e.g. Flerov 1952; Zai 1964; Dzięciołowski 1969; Sablina 1969), but little objective work on shelter-seeking behaviour *per se* has been carried out on red deer. Wind and temperature act together in affecting heat-loss (Blaxter *et al* 1963; Moen 1973) and, together with precipitation and solar radiation, are most important in affecting wild deer in winter. Deer respond to each factor according to the severity of the others. Thus, wind speed is probably dominant to temperature in inducing shelter-seeking behaviour on open-hill ground, but the reverse is likely to be true in thick woodlands, and various studies have shown that site characteristics do modify the importance of different factors. Some deer species may seek areas with the most 'comfortable' or even temperatures e.g. red deer (Darling 1937), black-tailed deer (Taber & Dasmann 1958), white-tailed deer (Verme 1965; Ozoga 1968) and mule deer (Loveless 1967), but this was not the case in Staines' (1976b) study on red deer in north-east Scotland. Here, resting red deer were found in proportionately more shelter as chilling conditions increased, and they put up with worse conditions when feeding than when they were resting; shelter was judged to be the limiting factor affecting distribution over the whole winter period. Cumming (1966) and Robertson (1967) also found that roe deer in Scotland sought shelter from strong winds, and Davidson & Kean (1960)

state that permanent occupation by red deer of high tussock grasslands in New Zealand was prevented because of the frequency of gales. Moen (1973), on theoretical grounds, considers that wind speed is likely to be the most important factor in making *Odocoileus* spp. seek shelter, and these species are usually found no more than a few hundred yards from cover of some sort (Taber & Dasmann 1958; Dasmann 1971).

Deer with access to woodland seek shelter in heavy rain (e.g. mule deer, Linsdale & Tomich 1953; *C. elaphus roosevelti*, Harper *et al* 1967; roe deer, Robertson 1967), but since shelter from rain is generally unavailable on open-hill ground in Scotland, sheltering from the wind under such conditions is probably more important (Staines 1976b).

Red deer in Scotland probably suffer from heat stress in summer to a limited extent (Darling 1937; Staines 1974, 1976b) and, under experimental conditions, have a lower capability to retain water than black-faced sheep (Maloiy, Kay, Goodall & Topps 1970). There has been little experimental work on the physiological tolerance limits of red deer.

Red-deer range throughout Scotland is quite diverse in its shelter characteristics. Few attempts have been made to classify areas in terms of natural shelter (cf. Staines 1970; Jackes 1973; Staines, Parish & Crisp in prep.) and there are few quantitative data to support them (e.g. as in Verme 1965, 1968; Ozoga 1968), or to compare the shelter characteristics of different areas. It is important to understand the relationship between shelter and food supply, for areas of good shelter from storms should not necessarily be ones of high food-quality, as these are likely to be heavily utilised before storm-weather approaches, leading to severe overgrazing and subsequent deer mortality e.g. Mitchell & Staines (1976). We need to know more on the range of weather factors to which red deer are susceptible, their ability to find shelter from these, the quantity and quality of shelter in different areas, and the subsequent effect on their energy exchange.

3.2.3 Disturbance

Disturbance alters the behaviour of animals and may affect their physiology, population dynamics and ecology (Geist 1971). The unpredictability of a source of disturbance may cause loss of weight, loss of appetite, neurosis, susceptibility to predators, lower reproductive capability and even death (see discussion by Geist 1971). Geist also quotes Zhigunov (1961) in relating disturbance to physiological stress and the outcomes of this in reindeer, the critical times of the year being during calving, late lactation and when they were under other environmental stresses such as harassment from insects or during very cold spells in winter.

Disturbance can also cause an animal to leave an otherwise favourable area to occupy a less favourable one. For example, Batcheler (1968) found that deer in one part of New Zealand moved to a less-preferred habitat,

became more secretive and also nocturnal in habit when continuous hunting started. He states that animal performance then declined, with animals in poorer condition and having lower reproductive rates. In Douglas's later study (1971), the animals had reverted to daytime feeding on open grasslands two years after hunting stopped. Increased wariness of deer during hunting seasons and alterations in their activity pattern have also been noted in Tule elk (McCullough 1969) and in white-tailed deer (Behrend & Lubeck 1968; Marshall & Whittington 1968; Roseberry & Klimstra 1974). Reactions to hunting vary according to habitat; in woodland, red deer remain, if possible, and become secretive (Jefferies 1894; Lloyd 1970); on open ground they group together and run away in file from the source of disturbance (own unpublished data). Staines (1970), however, whilst accepting that hunting modified dispersion patterns for a few days, found no evidence that heavy shooting was the reason for seasonal differences in dispersion by red deer in north-east Scotland.

Other land management practices such as burning and rounding-up sheep and cattle (Darling 1937; Hood & Inglis 1974) are also likely to influence dispersion, but how long these effects last is not known. For instance, in a preliminary study on the disturbance to red deer by hill walkers in north-west Scotland (Brathay Exploration Group 1974), little prolonged effect was found provided the hill walkers remained on paths. If disturbed, the deer tended to move only short distances, and often were found grazing close by the footpaths where walkers had been only a few minutes previously. Altmann (1956) found increased wariness when animals were near obstructions (e.g. fences) as did Rowe-Rowe (1974) for blesbok (*Damaliscus dorcas phillipi*), and irritability is often associated with weather factors e.g. high humidity (Darling 1937), low atmospheric pressure (Loveless 1967) and high wind speeds (McCullough 1969). We have found that red deer quickly become used to man's activity, particularly if it is consistent and not harmful to them and that, generally, females are more wary than males, as Hood & Inglis (1974) found also in white-tailed deer. Geist (1971) suggests that animals learn to avoid predictable disturbances; undoubtedly they also learn to live with them. McCullough (1969), although recognising the effect of man in restricting the distribution of Tule elk, makes the obvious, but valid, point that disturbance will only cause animals to move permanently away if there is another suitable area nearby. The response to disturbance is probably dependent on the strength of the stimulus, the alternatives facing the animal and learning from previous encounters.

Apart from man and competitive grazers (3.2.3.1), insects and predators are also important in affecting deer dispersion. Red deer are irritated by biting insects (Blaxter *et al* 1974) and may seek higher, insect-free ground in summer (Darling 1937), but they are probably less disturbed by them than, for example, reindeer (Zhigunov 1961) (see comments in 5.3.4). Adult red deer

in the British Isles have no natural predators (see 5.3.5), but golden eagles (*Aquila chrysaetos*) will prey on young calves. Disturbance from eagles causes flight (Cooper 1969; Staines 1974), and Clutton-Brock & Guinness (1975) have described differences in maternal behaviour at, and soon after, parturition which affects the short-term local distribution of deer. Nursing mothers were found apart from other hinds, and the authors suggest that this may be an adaptation to keep calves away from areas of high deer density which would have been more likely to attract predators.

Theoretically, any disturbance must have an undesirable effect in that it raises metabolism and thus the "energy cost of living" (Geist 1971). However, the overall effect depends on the quality of the other features of the environment. Even minor disturbance may impose a significant energy cost if the animal is already under energy stress from other causes.

If we know how much disturbance keeps animals from an area, this has obvious management implications. With increasing recreational pressure on the Scottish Highlands, the Lake District and Exmoor (where the main populations of red deer occur in Britain), it is clear we must know something more of the good or ill effects that disturbance can have.

3.2.3.1 Interactions with other grazing animals. Competition between two or more grazing species can be direct or indirect. Individuals may avoid each other or their signs (e.g. dung) or there may be agonistic behaviour between them. Alternatively, they may eat the same plant species. This alone does not necessarily mean competition, for they may be complementary, taking different parts of the same plants or the same plants at different times of year, with a succession in grazing such as has been well documented in African ungulates (e.g. Bell 1972). Heavy grazing by one species may help another by keeping the plants in a more-suitable form (e.g. physiologically young and nutritious). In this case, possibly only one partner benefits.

There is little knowledge on inter-relationships between different herbivores in the British Isles, most studies having been autecological in approach. Black-faced sheep have the same diet qualitatively as red deer (Colquhoun 1971; Hobson *et al* 1976), mountain hares (*Lepus timidus*) eat heather, blaeberry and *Eriophorum vaginatum* (Hewson 1962), as do red deer (Staines 1970 and in prep.), and heather is the staple diet of red grouse (*Lagopus lagopus scoticus*) (Jenkins, Watson & Miller 1963); but little advance has been made towards understanding problems of competition between these species. Savory (1974) and Hewson (1976) reported that deer, grouse and mountain hares showed distinct preference for heather stands of different age or height, hares using the youngest and deer the oldest. However, they judged usage by the frequency and abundance of droppings, and red deer rest in long heather in winter (Staines 1976b), but may not necessarily prefer it for food.

It is traditionally believed that hill sheep compete with, but that cattle are complementary to, red deer. Hence, we have seen alternating fluctuations of high sheep and high deer numbers on estates depending on 'fashion' or economic circumstances prevailing at the time (see Lowe 1961; Colquhoun 1971). McNally (1970) recounts how deer returned and increased in numbers when sheep were removed from a deer-forest in north Scotland in the late nineteenth century. Although it was deliberate action on the part of the landowner to increase deer numbers, the inference was that there was competition, and deer returned when competitors left (see also Boyd 1970). Ahlén (1975) believes that domestic livestock (cattle, horses, and sheep) adversely affected red deer in Scandinavia by reducing the supply of high-quality winter browse, especially in areas with much snow; when the grazing of domestic livestock was abandoned, the meadows and rough grazings became highly favoured by deer. Colquhoun (1971) found that there were quantitative differences between red deer and black-faced sheep in the proportions of species eaten, in the amount of time spent on various communities, in diurnal and nocturnal behaviour and in altitudinal movements. He states that the grazing ecology of sheep and deer "is much less similar than commonly supposed". However, such findings still do not preclude competition between the species, and an experimental approach is needed to isolate its possible importance.

Combinations of grazers may be more beneficial to each other than one species alone (Dasmann 1965). One can appreciate this situation arising in a 'natural' setting where the species have evolved together, but in Great Britain we have relatively few large indigenous grazers in proportion to domestic species. However, Lowe (1969) and Ball (1974) state that, on Rhum, after the sheep stock was removed and muirburn was stopped, there was a decrease in the extent of the preferred, 'first-class' grazings. The suggestion is that red deer alone were not able to maintain these pastures, even with increased deer densities. Cameron (1923) felt that both sheep and cattle are beneficial to red deer in that cattle "keep the black land trimmed" and sheep "the green land green", whereas deer are unable to do this by themselves because of their "fickle feeding habits".

It is not known if there is important competition between different deer species in Great Britain. Vladyshevskii (1968) suggests that, because red-deer and roe-deer densities are inversely related in the Ukraine, there is competition between them; at high red-deer densities he considers that roe deer are "driven out from the more favourable habitats" (translation). A similar inverse relationship may occur in Austria (Wildash 1951). In Scotland, Batcheler (1960) found that red deer were associated more with the younger stages of forest growth, and that they were "more numerous in forest stands of smaller median diameter than were fallow deer". He concluded that habitat structure and differential habitat selection affected the relative abundances of red deer, roe deer and fallow deer (*Dama dama*) more

than inter-specific competition.

Inter-specific competition and animal-range relationships are complex, and we need more information about the inter-relationships amongst all the grazing animals and their environment rather than treat each species in isolation.

3.2.4 Social behaviour

In addition to the process of habitat selection, social factors are involved in the arrangement of deer within their habitat. This is usually in the form of interactions between individuals, families, or 'groups' rather than populations *per se*. The commonest mechanisms recognised are territorial behaviour, and various forms of home-range and spacing behaviour. Any behaviour which limits an animal to a particular area is likely to affect performance to some extent. Hence, it affects population dynamics through reproductive success (e.g. competing males) and dominance hierarchies give a greater chance of survival to the dominants. A population is heterogenous, each individual having a differential survival potential, and a different contribution to make to the population through reproduction. The extent to which limitations on distribution by social behaviour affect performance is largely due to the proximal factors, usually nutrition, but could also possibly be due to 'social-stress' factors operating more directly on the animals themselves (see fuller discussion by Watson & Moss 1970), although there is little evidence for this in deer species.

Understanding behavioural limitations on dispersion is also important for predicting habitat-use. The extent to which an animal aggregates could markedly modify vegetation patterns, and the effect of a continual low-level grazing-pressure may be entirely different to an intermittent, high-level one.

3.2.4.1 Social organisation. Red deer are social animals and live in groups. In general, except during the rut, the sexes live apart (see pp 20-21). The basis of social organisation in hinds is a matriarchy (Eygenraam 1963; Lowe 1966; Knight 1970; Clutton-Brock 1974; Franklin, Mossman & Dole 1975), with groups consisting of a matriarch, her mature daughters and their dependent offspring of both sexes. Hinds associate more with their own kin than with non-relatives. Individuals have overlapping home ranges (Lowe 1966; Staines 1970; see also 3.2.5), and Clutton-Brock (1974) states that groups have "a well defined home range which overlaps with those of other groups"; the groups may join in temporary associations, generally linked through kinship. Franklin *et al* (1975) found also that the home range of a herd of Roosevelt elk overlapped with that of other herds, although the central part of the range was exclusively used by them.

The calf's exploratory behaviour may start within six months (Lowe 1966), and with temporary and often active dissociation of yearlings at calving and during

the rut, more independence is gained. Yearlings at this time may be found grouped together in small bands, and final independence from the maternal group was attained by the third year in studies by Lowe (1966) and Franklin *et al* (1975), and the fourth in that by Eygenraam (1963). Ahlén (1965a) thinks it occurs earlier in red deer in Sweden.

Some authors have implied social order within groups larger than the family unit (e.g. Darling 1937; Altmann 1952; McCullough 1969). This probably arises in part from the observation that in certain study areas from a few hectares in size (Watson 1971; Watson & Staines in prep.) to several square kilometres (e.g. Darling 1937; McCullough 1969; Mutch *et al* 1976), the total number of deer is relatively constant despite the number and size of the groups altering daily; also, the deer do not freely move out of these areas. For example, Watson (1971) found that the number of stags in one area remained fairly stable (18-25) over a 17-year period despite mortality and recruitment. Constancy in numbers suggests, in fact, that the areas in question are fairly natural 'deer-catchment areas', and have sufficient resources to support at least that number of deer. Also, dominance hierarchies are found in these large groups (Altmann 1952; McCullough 1969; Lincoln *et al* 1970; Gossow 1971; Watson 1971; Topirski 1974); they are usually linear in males but variable in females. Gossow (1974) regarded the winter herds of red deer in alpine regions of Switzerland as "closed" with a well-defined hierarchy, whereas the summer ones were "open" allowing a lot of mixing with little social conflict or evidence of hierarchies. Most of these studies, however, involved an artificial situation, such as supplementary feeding, and little has been done relating dominance to dispersion and utilisation in the more 'natural' situation (cf. Clutton-Brock & Guinness in progress).

However, that these larger groups are social entities has been questioned, since studies of marked animals have shown that individuals do not associate permanently with deer other than close relatives (Schloeth 1961; Lowe 1966; Knight 1970). Franklin *et al* (1975), regarded the herd of Roosevelt elk they studied as "a semi-stable association in which elk entered and left the group freely" (see also Harper *et al* 1967; Craighead *et al* 1973). Deer may aggregate because of some particular resource rather than for social attraction, and Knight (1970) suggests that in these cases the groups should more properly be termed aggregations, since individuals do not associate for social reasons alone. Nevertheless, this does not preclude social responses such as dominance hierarchies and leadership occurring within the aggregations. Since individuals have overlapping home ranges, they meet their nearest neighbours (probably relatives) more frequently and a stronger social bond or association develops than with those from further away.

Group integrity or constancy as implied by Darling and others is probably, therefore, an interaction between

social attraction (within the family), gregariousness, and the relative attractiveness of particular resources within their habitat. The size of the groups, and the extent to which they join or split into larger or smaller units, depends on the dispersion of their resources within the overall range.

3.2.4.2 Group size. This is very variable within and between populations. Generally, animals living on open ground are found in larger groups than those living in forests (Dasmann & Taber 1956; Peek, LeResche & Stevens 1974; Franklin *et al* 1975). Even within these habitat types mean group size varies considerably. For example, on hill ground on Rhum it was nine in spring and eleven in summer, whereas it was 40 and 35 in the eastern (Lowe 1966) and central Highlands (Staines 1974) respectively. Lowe suggested that the smaller group size on Rhum is probably due to the well-dispersed pattern of shelter and preferred vegetation types. This observation is supported by Clutton-Brock (1974), who found that group size in one area of Rhum altered depending on weather and the food resources being utilised at the time. Hence, deer frequently gathered in compact groups to feed on the herb-rich grasslands, but were generally widespread and in small groups when feeding on *Molinia*-dominated hill pastures, or when sheltering from high winds. Other authors have also related variations in group size to weather conditions (Flerov 1952; Sablina 1969; Gossow 1971), season (Sablina 1969; Knight 1970) and food availability (Altmann 1956; Gossow & Schürholz 1974).

In some areas in Scotland, certain hills often have large groups of resting deer, others only small groups. Large groups of red deer tend to occur in more-open areas with a clear view, whereas in places where only small or medium-sized groups are seen, the ground is often broken and visibility restricted (Staines, Parish & Crisp *in prep.*). Large group-size may give more protection from predators, or disturbance, in open areas (see Hamilton 1971; Vine 1971; Geist 1974; Jarman 1974). When groups come down from resting sites on the open hill-sides, they often split into smaller units as they pass through the woods, but reform into larger groups on the river flats.

Largest groups often consist of females (Ahlén 1965a; Harper *et al* 1967; Staines 1974), but of males in the high-alpine populations in Switzerland in summer (Gossow 1971). Adult males are often found singly or in very small bands (Altmann 1952; Ahlén 1965a; Knight 1970). Boyd (1970) reported that, when on spring migration, young males may be found in bands of 300-400, adult males 2-20, and females and offspring 10-50. Differences in group size between populations may be related to density, to some extent, but this view was discounted by Sablina (1969) in the USSR. Large groups were found by Staines (1970) even though density was low.

Until the relationship between group size and the different environmental factors is better understood, we will

not be able to predict with any certainty the type of deer usage an area will get. This is important since we may want to alter the structure of the habitat to ensure a more-even grazing pressure or to reduce a high one in certain vulnerable areas. We also need to know the effects of varying density on this situation, for a general lowering of deer density may not affect all the range to the same degree, because of the grouping behaviour of the deer.

3.2.4.3 Group composition. The extent to which the sexes remain apart outside the rutting season is variable. According to Lowe (1966), 34% of deer counted during spring on Rhum were found in mixed groups, compared with 41% at Glen Fiddich and Invermark in east and north-east Scotland (see Fig. 1 for areas). Staines (1970) found that the proportion of stags in stag-only groups averaged 56% throughout the year in Glen Dye, adjacent to Invermark, whilst Jackes (1973) found that segregation was almost complete on an area in Glen Goibhre, 93% and 96% of stags being found in stag-only groups in the spring of two succeeding years. In the Crimea only 18-29% of stags were in all-male groups and 50-56% of hinds in all-female groups (Yanushko 1957), and in Holland 70% of stags were in all-male groups in Eygenraam's (1963) study. Altmann (1956) and Gossow (1974) found more mixing of the sexes on winter range when animals were found in fairly restricted areas near artificial-feeding sites, and Staines (1971) found that the greatest amount of segregation was between the older, more-dominant stags and the hinds, this being 67%, 73%, 51%, 59% and 87% from January to May respectively. Similar conclusions can be drawn from Franklin *et al* (1975).

In Scotland, groups of hinds tend to have higher proportions of lactating (milk) or non-lactating (yeld) hinds than one would expect at random (e.g. Lowe 1966) and, in spring and summer, yeld hinds usually occur at higher altitudes than milk hinds. He attributed this to their better physical condition enabling them to forage more widely. Our own observations in Glen Feshie, however, show that groups contain different proportions of yeld and milk hinds, irrespective of altitude. "Nursery herds" have been reported by Gossow (1971), and Peek & Lovaaas (1968) and Mutch *et al* (1976) found that, in general, the smaller groups contained larger proportions of calves.

Even within groups, similar types aggregate and may occupy different positions in the group. For example, when resting, adult males tend to be found nearer to other adults, and the younger sub-dominant animals tend to be at the periphery and, if on a hillside, at the top part of the group (Staines, Parish, Crisp & Stevenson 1974).

It is not clear, therefore, whether individuals of a similar kind associate because of social factors, or because they have different requirements which are best met only in different parts of the overall range, or, more likely, because of both (see also 3.2.4.4).

3.2.4.4 Factors affecting the segregation of the sexes.

In Scotland the sexes occupy traditional areas which are often geographically distinct. Few studies elsewhere have considered this segregation in detail, but Peek & Lovaas (1968) found varying ratios of males to females in different parts of the Gallatin winter range in Montana. They quoted Murie (1951 p 275) and Anderson (1958) in relating the distribution of adult males to the higher, remote areas away from the main herd in winter, but they made no comment on differences in habitat type within their study. Franklin *et al* (1975) suggest that adult males are often solitary and used the coniferous-forest areas more than females, and Harper *et al* (1967) found differences in food selection by males and females which they attributed largely to the occupation of different areas; males remained in the remoter parts of the "brush" and only occasionally visited the prairie. Ahlén (1965a) made more relevant comment on this problem when he stated that males were found on sub-optimum areas surrounding the females; also that males were more wary, and that females were sometimes found on better soils. Watson & Staines (in prep.) similarly found that females were associated more with better rock types than were stags in north-east Scotland, and that they occupied ranges with greater areas of better-quality grassland. Subsequent work has supported the likelihood of differences in food quality between the sexes, and on Rhum and in the central Highlands hinds ate food higher in % nitrogen than stags during autumn, winter and spring (Staines & Crisp, in press; Staines, Parish & Crisp in prep.). In winter, stags on Rhum tended to eat more *Calluna* and broad-leaved grasses but less sedges than did hinds. In the central Highlands stags ate less grasses and sedges than hinds and, in contrast to Dzięciofowski's (1969, 1970a) Polish findings, more *Calluna*.

Jacks (1973) categorised stag areas as having a predominance of Callunetum and areas of microtopographic shelter. She characterised hind areas as affording a "wider choice of vegetation types than those used by stags . . . and a high proportion of greens". On the basis of the likely difference in nutritional requirements, she suggested that stags selected areas for shelter, whereas hinds selected for better-quality food. Latterly, Staines, Crisp, Parish & Stevenson (in prep.) have found little difference in shelter quality when comparing actual sites where stags and hinds were found resting; during very bad conditions, hinds were often in better shelter. If hinds are in better condition than stags during winter (Table 9), it may enable them to forage more widely; when conditions are bad they can move further to find suitable sheltered spots. However, there are no quantitative studies of daily movements which could verify this point.

As the stags are polygamous, and the hinds need better food over winter because of pregnancy and initial calf survival, it would not be too surprising if mechanisms had evolved whereby the females were found in the better environments. However, the way in which they

maintain their areas is as yet unclear and experiments or surveys over a wider variety of habitat types than already studied are needed to separate cause and effect. There may be differential habitat selection by the sexes, or a spatial separation based on passive avoidance or agonistic behaviour, or both. There may be long-term dominance by hinds, even though in encounters stags are usually dominant. Examples of hinds inhabiting areas previously used by stags are quoted in Darling (1937) and Watson & Staines (in prep.), and it is generally recognised that stags are the initial colonisers (Darling 1937; Davidson & Kean 1960; Ahlén 1965a) but that hinds subsequently move into these areas.

3.2.5 Home range

We use home range as being "the total area with which an animal has become familiar, including seasonal home ranges, excursions for mating, and routes of movement" (the "lifetime range" of Jewell 1966).

3.2.5.1 Size. We must assume that a home range includes all the environmental factors necessary for an animal's existence, hence its size indicates the nature of the animal's resources. Great variation in size of home range occurs between populations of red deer, being obvious in comparisons of non-migratory (Craighead *et al* 1973; Franklin *et al* 1975) and migratory (Boyd 1970; Harper *et al* 1967) populations; in the latter, there can be more than 48 km between wintering and summering areas (e.g. Knight 1970).

Yanushko (1957) found that, from June to August, six stags in the Crimea occupied an area of only 5-6 ha and none had a range of more than 10 ha. Gibb & Flux (1973) in New Zealand state that the home range of individuals was only "a few km across" and few tagged animals were found more than 8 km away; these were all young males. In Great Britain, Lowe (1966) states that the home range for marked deer on Rhum was 800 ha for stags and 400 ha for hinds, but Staines (1970, 1974) showed that the home ranges of hinds in north-east Scotland could be more than 16 times as large. Although possibly there were differences in the methods for measuring home-range sizes in these British studies, they probably do reflect the marked differences between the areas. The distribution of shelter was the likely reason for the large annual home ranges in Staines' (1970) study, and Lowe's (1966) suggestion that a diverse habitat with many small feeding and sheltering areas makes for smaller home-range size seem reasonable. This idea needs testing, for it could have important management implications, enabling suitable deer habitat to be developed, either for the deer themselves, or to influence utilisation. In woodlands, home ranges are thought to be smaller than those on the open hill, but reliable information for Great Britain is lacking.

Home-range size varies between the sexes (e.g. Lowe 1966), males usually having larger home ranges than females. With Scottish red deer this difference is not

surprising, for, in winter, stags usually occupy areas geographically lower down the valleys, but in summer they may be at higher altitudes (Darling 1937; Lowe 1966). Similarly, stags may make long treks to their traditional rutting-places which may be outside their normal wintering or summering areas (e.g. Whitehead 1960; Lincoln *et al* 1970). Recoveries of marked deer (Red Deer Commission Annual Report 1975) have confirmed that stags move further than hinds, with a maximum distance for one marauding stag of 35 km from its place of tagging. However, stags may use a smaller area than hinds in winter (Staines 1974).

3.2.5.2 Tradition. During the rut, stags often return to a very localised area (Flerov 1952; Whitehead 1964, pp 59-66; Lincoln *et al* 1970). This fact has not been demonstrated for the central Highlands where home ranges are generally larger, but anecdotal evidence from stalkers who recognise individual stags that rut in similar places each year suggests that it probably holds true here also.

In migratory populations the routes used are often traditional (Murie 1951), as are the relationships between summering and wintering ranges (Knight 1970; Craighead *et al* 1972). Most individually-marked deer in these latter studies occupied a similar part of the gross seasonal-ranges each year, and, although they sometimes mixed with other populations on the summer range, they segregated during the autumn migrations (Murie 1951; Knight 1970). Staines (1974) gives an example where some of the wintering area for part of a population was cut off by a deer fence; from marked animals, he deduced that the animals went round the end of the fence, through ground occupied by other deer and back to their original wintering area, a distance of about 17 km. Members of the original population must have been dead, and he concluded that this movement had been maintained by learning from older animals.

3.2.5.3 Maintenance of home range. Deer are difficult to move out of their home range (Leopold *et al* 1951; Marshall & Whittington 1968; Staines 1974), and this implies fidelity to an area. Dunnett (1974, 1975) could not change the day-time distribution of

stags in winter by diversionary feeding, although nocturnal distribution was altered by 3 km. Data from Rhum and Ross-shire suggest that most deer move very little from their place of birth (Lowe 1966; Staines 1974; Red Deer Commission Report 1975).

Although it is known that deer can recognise and respond to natural features (Darling 1937; Miller 1974), it appears that the selection and maintenance of home ranges depend on social as well as habitat factors. For instance, Lowe (1966) found that individuals have different spheres of dominance over each other depending on their positions in their overlapping home ranges. When animal A was in the centre of its range and interacted with animal B which was at the edge of its range, A was dominant to B. There was a reversal of dominance when B was in the centre and A was at the edge. Graf (1956) states that Roosevelt elk of both sexes showed "sign-post" activity in some areas. He suggests that this may be territorial marking and "may serve to locate the closely knit family groups in the event of separation", and also that it may also act as a sign-post against strangers. During the rut, in areas where marking occurs there are no groups of associated males harassing the dominant male, but this is not the case in areas where "territorialism" is missing. He suggests a possible difference in behaviour between woodland and open ground. Marking has also been observed in British red deer in woodland (Chard 1958), and in North American wapiti (Harper *et al* 1967; Franklin *et al* 1975), and is known in other woodland species such as roe deer, fallow deer, black-tailed deer (Miller 1974) and white-tailed deer (Moore & Marchington 1974). The sites of wallows (Jefferies 1894; Altmann 1952; Flerov 1952; Delap 1970; Lloyd 1970) and the 'soiling pits' known in English folk lore (Jefferies 1894; Lloyd 1970) are traditional, and could be places for scent marking. These places could be similar to the digs, or scrapes, reported by Graf (1956).

Information on behavioural factors limiting distribution is scant, and detailed investigations are lacking. Possibly this lack is because of the difficulties involved, particularly in woodland, and the long time-scale needed for such studies.



Plate 3A

Part of a large group of stags on closely-cropped *Calluna* in late March. Biggest stags tend to occur in the central part of a group, and smaller ones at the edge. Adult stags, and hinds with their dependents, usually occur in separate groups, and live in different areas for most of the year. In winter, some areas are used mainly or exclusively by stags, and others by hinds.

Plate 3B

Small group of hinds and young stags on wet, rushy grassland. Young stags usually become independent of the maternal groups by their third year. The ground occupied by adult stags tends to have less floristic diversity and a smaller proportion of good grassland, than the ground used by hinds.





Plate 4A

Part of a large group (c. 500) feeding on grassland and *Calluna* communities in a valley bottom in late winter. The size and composition of red-deer groups are influenced by several factors including habitat type; groups tend to be larger and more segregated on open range than in woodland.

Plate 4B

Hinds and young of both sexes in open woodland of *Pinus sylvestris* and *Betula* in deep snow. Heavy snowfall restricts movements, and feeding is mainly confined to dwarf shrubs, bushes and trees.





Plate 5

Samples of rumen material from red deer shot in winter, showing variation in diet. A typical sample from Rhum (upper left) consists mainly of grasses and sedges with some seaweed, whereas one from the eastern Highlands (upper right) has more *Calluna*, *Arctostaphylos uva-ursi* and ferns. Two samples from the central Highlands, taken from animals shot on the same day within 5 km of each other, show differences in selection within a relatively small area. Lower right consists mainly of *Betula*, *Calluna* and lichens, and lower left of *Pinus sylvestris* and *Calluna*.



Plate 6

Two types of woodland habitat used by Scottish red deer. Upper shows one of the few remaining natural pine forests in the central Highlands. There is an open canopy and extensive ground vegetation, and regeneration of *Juniperus communis* has occurred. The lower is an example in the western Highlands of the many plantations now being created on hitherto-open range. Despite fencing, these plantations are liable to permanent colonisation or to break-ins during winter by deer seeking food and shelter. They are especially vulnerable when previous wintering areas have been afforested, and when the movements of the deer between low-lying and higher ground have been impeded.



4. Impact on the habitat

The red deer, like any other herbivore with appreciable biomass and density, influences vegetation both in composition and structure. Because the distribution of red deer in Britain is broadly complementary to that of domestic livestock, consideration of their impact entails comparisons both with the situation where sheep or cattle are the main herbivores, and with the situation where all large herbivores are absent. Variation in impact between herbivores arises from differences in feeding habits, mobility and home range, treading, dunging and reaction to disturbance. It has been found convenient to consider woodlands separately, although recognising that impact depends, in the first place, on how the deer apportion their time between the vegetation types to which they have access; also direct effects are distinguished from those of the associated management practices.

Detailed examination of impact on cultivated land is outside the scope of this review, but it must be remarked that much damage can occur. Red deer readily feed in cornfields, meadows, pastures and arable crops, especially when little forage is available (McCullough 1969; Marshall 1970; Nannestad 1970; Clarke 1972), and potato tubers and grain can be important items in the diet (Jensen 1968; Dzięciołowski 1970a). In Scotland, Grant P.C.H. (1968) considered that relatively few deer were 'marauders', but this was judged in a context of farmland often protected by strongly constructed fencing and sited where 'marauding' was less likely. Indeed the lack of cultivation in deer-forests has ecological implications, affecting the type of habitat available to the deer and the usage it receives.

4.1 OVERVIEW OF STUDIES ON IMPACT

4.1.1 Studies in foreign countries and their relevance to Britain

A great deal of research has been done on the inter-relationships of the Cervidae and vegetation, especially in New Zealand, North America, and central and eastern Europe. Research has naturally been concentrated where deer are causing serious problems, but there is a danger of over-emphasising the environmental disasters and thinking they could all occur in Britain. The vulnerability of soils to nutrient loss and erosion, of plants to grazing and browsing, and of animals to nutritional and climatic stress, varies greatly between continents and between ecosystems, depending on which of the many processes involved are the most important. Thus, although studies done elsewhere may suggest consequences of red-deer presence in British habitats, and are valuable for the ecological principles, concepts and methods they impart, they must be supplemented by systematic research within Britain to obtain the certain knowledge needed for management.

In New Zealand, the impact of red deer, first introduced in 1851, has been especially severe (Howard 1964). Together with other introduced mammals, they caused great changes in the composition and struc-

ture of the native woodlands, virtually eliminating some species and vegetation types e.g. sub-alpine scrub, and inducing large-scale soil erosion and flooding problems (Howard 1967). However, Howard stresses that New Zealand was highly vulnerable to herbivorous mammals, the flora having evolved in the virtual absence of browsing, the soils being thin, the rocks soft, the topography steep and the rainfall heavy.

Research work has had a botanical emphasis, with detailed classification of the forest types and determination of their successional position in relation to ungulate use (Wardle & Hayward 1970; Wardle, Hayward & Herbert 1971). These workers developed susceptibility ratings for plant species and associations, and chose 'indicator species' representing the range of reactions to browsing, for use in determining the degree of modification a forest had sustained. These parameters have not as yet been related to deer densities, although assessment by pellet-group counting has begun (Tustin 1973). Holloway (1950) and Howard (1964) contended that botanically stable communities would arise from the unpalatable or browse-resistant species remaining after the more-susceptible plants had been eliminated, carrying lower herbivore densities than the original vegetation. However, with widespread control occurring, and measurements of deer density few, it is difficult to be sure that self-adjustment of deer numbers has occurred in New Zealand, such that the modified communities can perpetuate themselves. The actual consequences of deer presence have little relevance to Britain and the North-Temperate zone, for the reasons cited above, and because the year-round availability of browse in evergreen and predominantly broad-leaved forest allows relatively rapid increase in numbers unchecked by seasonal stress (Wodzicki 1963).

In North America, the impact of cervids is well documented, and several instances of population increases followed by catastrophic changes in vegetation and high mortality have been described (Rasmussen 1941; Aldous & Krefting 1946; Bartlett 1955; Klein 1968). The authors agree that the populations, of mule deer, moose, white-tailed deer and reindeer respectively, increased rapidly because predation and shooting control were absent or at low levels. The palatable plant species were then eliminated or so depressed in production that the animals were starved. Wapiti, however, have not caused such great problems (Taber 1965), and, for various reasons, these classic demonstrations of ecological principles being fulfilled may not apply to red deer in Britain. Three of them took place on small islands from which emigration was difficult, and in the fourth mule deer were involved. This species tends to remain in its normal home-range even when the good forage is used up (Taber & Dasmann 1958), and is also a more-specialised feeder than the wapiti, being known to die in areas without browse where the latter thrive (Murie 1951).

A feature of American research on cervid-habitat relationships has been the development of methods of assessing range condition and herbivore usage in terms of 'increaser' or 'decreaser', 'preferred', 'staple' or 'low-value' species, and their age, form-class or degree of utilisation (Dasmann 1951; Habeck 1960; Patton & Hall 1966). These methods have been used over large areas such as California (Longhurst, Leopold & Dasmann 1952). Emphasis has also been given to maximising the production and availability of browse (Davenport, Switzenberg, vanEtten & Burnett 1953; Shafer 1965), and to examining interactions between herbivores, with measurements on their utilisation of sites and plant species (Stevens 1966; Skovlin, Edgerton & Harris 1968).

The prevailing motivation of research in central and eastern Europe on red-deer impact is the protection of woodland from excessive damage. Alongside practical work, such as testing repellents and calculating economic losses, there have been fundamental studies on feeding, combining measurement of the plant biomass available and its utilisation with estimation of the intake by rumen analyses (Dzięciołowski 1969). Comparatively little work has been done on the effects of deer on the composition of plant communities.

As in North America, much attention has been given to carrying capacity. The methods of site evaluation developed by Ueckermann (1951, 1957) and others, are based not on direct observations of plant form or trend at a site, but on characteristics such as the species of tree present, the type of regeneration required and the snowfall experienced, and use quantities and rankings derived from detailed studies at other sites. Perhaps the potential immediacy of heavy damage in Europe, for instance when bark-stripping begins, explains this difference from America, where impact from *Odocoileus* develops more gradually.

The findings of this research are very relevant to Britain because similar plant communities are involved; they will be considered in 4.2 and 4.3. Furthermore some of the information could not readily be obtained here because relatively few woodlands are freely available to red deer, but, with increasing afforestation, knowledge on the likely impact of deer is much needed.

4.1.2 Studies in Britain

The little scientific research which has been done on deer impact is mainly recent, stimulated by the pioneering work of Darling (1955). Because of difficulties in monitoring usage over long periods, hardly any attempt has been made to relate trends in the composition of vegetation directly to the grazing received. Ball (1974) described the effects of protection from grazing in exclosures on the Isle of Rhum, and the trends in adjacent areas grazed almost exclusively by deer, but the amount of grazing was not measured; comparison with the previous mixed-grazing regime was made difficult because the herbivore biomass was greatly reduced initially and burning ceased. Welch (1974a, and in

prep.) studied succession between dwarf-shrub and monocotyledonous communities at a series of sites in north-east Scotland, some of which were grazed largely by red deer, and some by sheep and cattle.

More studies have been made on the utilisation of plants by deer. If the reactions of the plants are known, both individually and collectively, the long-term results of deer presence can be estimated. Seasonal utilisation of important species, including self-establishing tree seedlings, was observed in Glen Feshie, Inverness-shire, by Miller (1971), and Miles (1971) measured utilisation of *Molinia* and other species on burnt and unburnt ground on Rhum. Also in Glen Feshie, Miller & Cummins (1974) observed browsing on experimentally established tree seedlings. Rather more work has taken place on the impact of deer in woodland (Cooper 1967; Pellew 1968; Stickles 1971), probably because the economic consequences in this habitat are readily appreciated.

Several detailed studies on the occupancy of vegetation types have been made in different parts of Scotland, including Rhum (Nicholson & Charles 1969; Charles *et al* 1977), Glen Goibhre, Ross-shire (Jackes 1973), Ben Lawers (Colquhoun 1971), Glen Feshie (Staines 1974; Staines, Parish & Crisp in prep.; Welch 1971a), and Glen Dye (Staines 1970 and in prep.). Although there was either no access to woodland, or very little extent of woodland in the range of these deer, the areas are typical of present-day Scottish deer-forests, and the findings on preference for particular plant communities enable tentative conclusions to be drawn about deer impact.

4.2 EFFECTS ON MOORLANDS AND GRASSLANDS

4.2.1 Composition changes

Various successions between dwarf-shrub heath and monocotyledonous plant communities, and between different types of the latter, have been demonstrated or inferred in Britain (Ratcliffe 1959; King 1962; King & Nicholson 1964; Gimingham 1964; Dale 1973) and continental Europe (Ahlfén 1965a; Westhoff 1967). It is established that the dwarf-shrub communities are replaced by monocotyledonous ones as grazing pressures increase.

In the studies on succession between these communities in north-east Scotland (Welch in prep.) the threshold densities of different herbivores causing depression of Callunetum were estimated. It is clear that red deer will rarely cause succession to monocotyledonous vegetation in open situations, and then only over a very small part of the range: two sites in Glen Feshie used over a four-year period by nearly 2 deer per ha, which must be close to the maximum density presently found in Britain, showed small but divergent botanical trends, with heather decreasing in cover and height only at the site where it had lower annual growth. Significant differences between the effects of equal biomasses of red deer and sheep on sites were not demonstrated, but equivalent densities of cattle seem to cause greater reduction of *Calluna*, perhaps because of the coarser

grazing and the nature of the dung (Welch 1974a, and in prep.). The impact of herbivores depends also on their dispersion and which vegetation types they choose to utilise. Because red deer occupy their whole range more evenly (compare Charles *et al* (1977) and Welch (1971a) for deer, to Hunter (1962) and Rawes & Welch (1969) for sheep), eat a higher proportion of *Calluna* and a lower proportion of grass than sheep on the same ground (Colquhoun 1971), and prefer to graze grassy Callunetum rather than pure Agrost-Festucetum (Welch 1971a), stocking exclusively with deer in the British uplands brings about a reversion of grasslands to dwarf-shrub heath. In contrast, cattle and sheep prefer Agrost-Festucetum, and have either maintained these grasslands, often on sites of former woodland, or created them from heath by utilising most heavily the sites with best soils.

On wetter soils the presence of monocotyledonous communities such as Juncetum squarrosi, Molinietum and Nardetum also depends on heavy grazing, but they do not attract utilisation intensive enough to impede succession to dwarf-shrub heath unless the overall stocking rate is high (Rawes & Welch 1969). Red deer never live at these high densities, and on hills grazed largely or exclusively by deer such communities are relatively scarce (McVean & Ratcliffe 1962). Molinietum is the most common probably because the abundant litter produced when *Molinia* has substantial cover in dwarf-shrub heath allows burning to take place so frequently that *Calluna* is reduced irrespective of the grazing pressure imposed (Nicholson 1974). In an unburnt *Calluna-Molinia* heath observed over a twelve-year period on Rhum, *Calluna* increased almost equally on deer-grazed and ungrazed plots (Ball 1974), and though deer usage was heavier on newly-burnt Molinietum (Miles 1971), it was not equivalent to the densities of sheep that depress *Calluna*.

The effects of animal densities on the inter-relationships of the various graminaceous communities of moist acid soils are not well understood. Darling (1947) considered that heavy sheep grazing allowed mat-grass (*Nardus*) to spread in Agrost-Festucetum, saying this had occurred on the lower slopes of Ben Lawers, and that cessation of grazing allowed the succession to be reversed. This was based, however, on a misunderstanding of Fenton (1937), and in exclosures in Nardetum in Snowdonia *Molinia* and heath species became dominant after about ten years (Dale 1973). Other pertinent observations and experimental findings are reviewed in Welch (1974b). Sheep, by their more selective grazing, are thought more likely to favour the development of unpalatable communities than cattle, but further long-term studies are needed to ascertain the frequency and extent of successions to unpalatable communities, and the herbivores and site conditions which most induce them.

Red deer, because of their lower stocking densities, are involved in successions between graminaceous communities only when using range grazed formerly or

currently by the other herbivores. On Rhum, the nutritional quality of the grazings apparently declined when deer alone remained after the removal of sheep and cattle (Lowe 1971). A differential reaction in Agrost-Festucetum was demonstrated by Ball (1974): species-poor Agrost-Festucetum became dominated by a few tall-growing grasses, other species, especially herbs, being reduced, whilst species-rich Agrost-Festucetum changed little, continuing to be closely grazed.

The effects of cessation of grazing depend on altitude, on soil type and on whether burning occurs. The standing crops of the plants previously grazed first increase, then successions begin. Woodland is the climax vegetation in most of Britain, and after 15 years trees are already growing in the Snowdonia exclosures (Dale 1973). Often much longer periods elapse before trees become established, as in the exclosures on Rhum, and at Moor House in the North Pennines of England (Welch & Rawes 1964), because of remoteness of seed sources and lack of suitable niches. In the meantime most grasslands revert to dwarf-shrub heath, with *Empetrum* and *Vaccinium* spp. taking the place of *Calluna* at higher altitudes. On base-rich soils tall herbs and ferns may become prominent.

4.2.2 Succession to woodland

In Britain, many upland grazings are treeless, but tree seedlings do become established when seed sources are available (Miles 1973; Kinnaid 1974). Miller & Cummins (1974) found seedling densities in Glen Feshie below 550 m to be 186/ha for birch (*Betula*), 58/ha for juniper (*Juniperus communis*) and 14/ha for rowan (*Sorbus aucuparia*), all less than 50 cm tall, and Holloway (1967) examining smaller areas more closely in Deeside found higher densities, largely of Scots pine. There is good evidence that the larger herbivores prevent these seedlings from developing into trees. Kinnaid (1974) described birch saplings up to 31 years old kept dwarfed by repeated grazing; nearly 90% of the saplings found in the Glen Feshie survey were browsed; and, in the same area, only 10-20% of naturally occurring birch and juniper seedlings escaped grazing over a twelve-month period (Miller 1971). Almost all the browsing in Glen Feshie was attributed to red deer, whilst on Deeside most damage to sapling trees was caused by sheep and deer, although red grouse and mountain hares were abundant at Holloway's study sites. The incidence of damage was shown by Miller (1971) to be significantly related to the height of the saplings above the surrounding vegetation. In a trial with planted birch and pine saplings, very few survived after four years due to being repeatedly damaged (Miller & Cummins 1974).

A relationship has been shown between the amount of browsing and the density of red deer both in Deeside and Glen Feshie. The overall stocking in the latter area is about 2,000 deer in 17,000 ha, but pellet-group and dung-volume measurements (Miller 1971; Welch 1971a, 1971b) suggest annual mean densities of 1 to 2 deer per ha at the study sites in the main glen. At

higher levels densities are less, and when pine and birch saplings were planted along an altitudinal gradient, only 64% of the pine and 86% of the birch were grazed above 630 m after two years, whereas at lower altitude none had escaped. Holloway (1967) found that at a winter density of 1 deer to 4 ha, estimated by pellet-group counts, few saplings of birch, larch (*Larix decidua*) or pine lived beyond ten years and all were kept short. At 1 deer to 25 ha saplings were surviving longer and some seemed likely to develop into trees, whilst tree development was little impaired by a winter density of 1 deer to 60 ha. Interestingly, Darling (1947), by intuitive observation, said densities should be kept down to 1 deer to 16 ha to allow woodland regeneration.

As Holloway points out, the amount of browsing is affected by factors other than animal density, including the quantities of browse on offer and the degree of preference for browse relative to other available foods. Since a substantial proportion of the diet of red deer is browse when they are free to choose (Fig. 2), deer given access to little or no woodland are likely to actively seek any obvious young trees establishing in open vegetation. European work e.g. Bjor & Graffer (1963) and Ahlén (1965a), confirms that deer, sheep and cattle prevent tree establishment, but no figures on the critical density of deer at which establishment would occur, given adequate niches and seed supply, have been obtained.

Differences between tree species in the amount of browsing received were demonstrated in Glen Feshie by Miller (1971) and Miller & Cummins (1974). Birch, being deciduous, was taken largely in summer; pine, being evergreen, showed much less seasonal variation, and juniper, being apparently less palatable, was grazed mainly during periods of snow-lie when little else was available. Hence the grazing imposed can influence the type of woodland that develops when succession is permitted. Darling (1947) stated that deer and cattle are not so effective in preventing regeneration as sheep, believing destructive capacity to be related to the number of mouths rather than to biomass or appetite. However, no systematic comparison between herbivores has been made, and it seems likely, considering the greater preference of deer than sheep for browse (Ahlén 1975), the greater mobility of deer (Colquhoun 1971), and their tendency to disperse more equally over the whole range than sheep, that deer are more effective than sheep, biomass for biomass, at impeding succession to woodland.

4.2.3 Controlling impact in moorlands and grasslands

Although the adverse effects of red deer particularly in preventing succession to woodland are recognised, they are largely accepted as the inevitable consequences of herbivore presence. It is known that winter feeding and concentration of culling can to some extent modify distribution, and fertiliser treatments have been given to selected areas of moorland (Nicholson 1971),

but the objectives of such activities have usually been those of animal husbandry rather than range management. Thus the main form of control is complete elimination by fencing. Management of hill ground for domestic livestock is further advanced; selected swards have long been fertilised, and recently reseeding scattered areas to attract animals to graze the intervening vegetation, and paddock systems to control herbage utilisation, have been evaluated (Nicholson, Currie, Paterson & McCreath 1968; Eadie 1970).

Our knowledge on red deer suggests the possibility that impact could be reduced by the use of physical or botanical attractants and deterrents or the provision of particular food. Planting shrub species favoured as browse but resistant to grazing e.g. broom (*Sarothamnus scoparius*) and gorse (*Ulex europaeus*) might reduce pressure on tree establishment, if done on a sufficient scale in a suitably dispersed manner, and with deer numbers initially controlled. McVean & Lockie (1969) describe two such trials, one at Lochmore in Sutherland, involving 120 ha of varied woodland with glades for wintering deer, but systematic study is awaited.

Impact could be controlled more readily if simple methods of assessing botanical trends, such as have been produced in North America, were available, to show for instance on a single inspection that *Nardus* is spreading in grassland, or that dwarf shrubs are replacing *Agrost-Festucetum*. Dzięciołowski (1970a) listed five species whose utilisation in Poland indicated an unfavourable trophic situation for the deer, and perhaps also unfavourable botanical change. However, because the number of plants involved in Britain is relatively small, and they are mostly perennials with quite wide ecological tolerances, compositional characteristics seem less likely to be useful here than structural features.

4.3 EFFECTS ON WOODLANDS

4.3.1 Browsing

Red deer utilise browse wherever it is available, and browsing is a major form of impact throughout their range. In Europe damage to woodlands from browsing and bark-stripping is widespread (Schulz 1960; Dzięciołowski & Pielowski 1967) and serious. It is difficult to ascertain its true cost because ideally long-term comparison of similar damaged and undamaged stands is required (Szczerbiński 1959). Ueckermann (1957) reported depreciations in value of up to 10%, and losses of up to £8 per ha were recently estimated in Germany (Phillips 1973). The amount of browsing is related to deer density (Ueckermann 1960).

Tree species differ greatly in their attractiveness to red deer as browse, and several authors have ranked preference (Table 5). Ahlén (1965a) believed such lists would not be stable because the needs and motivations of the deer, and the nature of the plants themselves, vary according to habitat. Dzięciołowski (1970c)

showed seasonal variation, *Quercus petraea* twigs being highly preferred in summer, less so at other times. However, the ranking orders obtained in different parts of Europe in different habitats correspond quite well: aspen (*Populus tremula*) and willow (*Salix*) are always highly preferred, and Sitka spruce (*Picea sitchensis*), alder (*Alnus*) and birch always little preferred. But Chard's observation (1966) that juniper is preferred above all else and Burckhardt's high ranking (1959) of this species contrast with Dzięciołowski's view (1970c) that it is starvation food. Disagreements like this are to be expected when the bases of ranking range from observations of damage to trees, to rumen analysis, to 'cafeteria' trials, to faecal analysis, and when the composition of the woods is so diverse. Dzięciołowski also considered *Pinus sylvestris* to have low palatability, and, in plantations in the northern Highlands of Scotland, this species was less affected by browsing than *Pinus contorta* or *Picea abies* (Badenoch 1971), whilst, in Glenmeanie Forest, Ross-shire, browsing was increasingly severe in the series *Pinus sylvestris*, *Picea sitchensis*, *Picea abies*, *Pinus contorta* (Stickles 1971). The severity of damage from browsing depends most on the age and size of the trees. Mature trees will normally withstand severe trimming of the lower side shoots without serious detriment to survival, growth or form (Holloway 1968). With younger trees there may be merely loss of increment or greater susceptibility to pathogens if the side shoots are lightly browsed, but, if the leading apical shoot is taken, mis-shapen trees yielding poor-quality timber result. At worst, under

heavy browsing, plantations fail or natural regeneration ceases, with the saplings dying or being kept permanently short. Vaněk (1956) and Holloway (1967), simulating browsing by clipping, found severity of damage to depend on the amount of shoot removed. Holloway also showed that damage was greater when clipping was more frequent, when it occurred outside the growing season, and on younger saplings, and Bjor & Graffer (1963) with cattle and sheep, and Kangas (1949) with moose, demonstrated that repeated browsing caused greater damage to conifers. Sablina (1959) claimed that the production of browse fell when consumption increased. The effects of repeated clipping in depressing height increment were found to be greater in conifers than in hardwood trees (Eiberle 1975). The browsing preferences of deer, their density, and the reaction of trees to damage will strongly influence woodland composition. Other contributory factors are the longevity of the trees and the length of the period of vulnerability of the saplings, which depends on their growth rates and the snow depths experienced. Although birch and Scots pine, the commonest trees in Scottish Highland woodland, are relatively unpalatable (Table 5), browse is so scarce, and animal densities are so great, that saplings are nearly always kept short and the woodlands fail to regenerate (Steven & Carlisle 1959; Kinnaird 1974); the scarcity of aspen, rowan and willow probably reflects previous grazing pressure. Elsewhere in Europe densities are such that the more-palatable species are selectively eliminated,

Table 5. Some ranking orders of browse preferences by red deer.
The data of Dzięciołowski (1970c) were obtained by 'cafeteria' trials on one male calf.

Author	Sablina (1959)	Dzięciołowski (1970c)	Bobek, Weiner & Zieliński (1972)*	Ueckermann (1960)	Ahlén (1965a)	Chard (1966)
Area	White Russia	Poland	Poland	West Germany	S. Sweden	NW. England
Highly preferred	Salix Populus tremula Fraxinus Quercus	Quercus petraea Salix caprea Sorbus aucuparia Corylus	Populus tremula Salix caprea Frangula alnus	Populus tremula Quercus borealis Abies Acer platanoides Fraxinus Quercus	Fraxinus Salix Frangula alnus	Juniperus Quercus borealis Pinus contorta Picea abies
Preferred	Sorbus aucuparia Betula	Acer platanoides Carpinus Prunus serotina Frangula alnus	Quercus robur	Pinus sylvestris Picea abies Fagus Pseudotsuga Larix	Betula	Larix Acer pseudo-platanus Pinus sylvestris Quercus Betula
Seldom or never browsed	Tilia Carpinus	Pinus sylvestris Juniperus	Tilia cordata Carpinus Betula	Picea sitchensis Alnus Betula	Alnus	Picea sitchensis Fagus sylvatica Alnus glutinosa

* includes roe-deer browsing

examples being ash (*Fraxinus excelsior*) in Scandinavia (Ahlén 1965a) and White Russia (Vrublovsky 1912), and silver fir (*Abies alba*) and beech (*Fagus sylvatica*) in Austria, Germany and Switzerland, which are replaced by Norway spruce (*Picea abies*) (Westhoff 1967). Compositional changes in North American woodland caused by cervids are well documented e.g. the decline of ground hemlock (*Taxus canadensis*) and white cedar (*Thuja occidentalis*), and the increase of the less-palatable balsam fir (*Abies balsamea*) in Michigan and Wisconsin swamps (Habeck 1960; McNeil 1964).

Comparison between deer and other herbivores in their browsing effects is speculative, as discussed in 4.2.2. When controlled, cattle and sheep are successfully grazed in forests in many parts of the world (Adams 1975), and, using knowledge on palatability and seasonal preferences, even regenerating woodlands or young plantations can be grazed without serious loss, as demonstrated in Strathdon in north-east Scotland where sheep had access to plantations of Norway and Sitka spruce (Ellice 1968). Bjor & Graffer (1963) studying hardwood and coniferous forest in Norway, said sheep did more browsing damage than cattle, but this was balanced by cattle causing more trampling damage. In these respects deer probably most resemble sheep because of their grazing action, hoof size and mobility.

4.3.2 Bark-stripping

Incidences, consequences and causes of red deer stripping bark have been the subjects of numerous publications. As yet there is no complete review, but Ueckermann (1960) in his book on browsing and bark-stripping by red deer gave many references, and Rijcken (1965), Ziegler (1967), Stubbe (1970) and Reijnders & Veen (1974) cite the more-recent studies. In central Europe assessments of the resulting losses in timber production date back to the start of the present century (Žáruba & Šnajdr 1966); the earliest work known to us focussing on bark-stripping was a book by Reuss (1888), and the earliest reference is in G. Turberville's *Noble Arte of Venerie or Hunting* (1576, pp 72-73). Shakespeare (1607) wrote:

"Yea, like the stag, when snow the pasture sheets
The bark of trees thou browsed'st"

Antony and Cleopatra Act I Scene IV.

4.3.2.1 Occurrence. Bark-stripping is most prevalent in central and eastern Europe, perhaps due to the type of habitat. In some other areas it is unknown e.g. most of Bulgaria (Petrov 1967; Stenin 1970); in others it is either unimportant e.g. north-eastern Siberia (Egorov 1967) or not customary e.g. North Africa (Meyer 1972). In North America bark is known to be taken from several species of tree, but the habit appears to have little economic significance (Murie 1951).

Trees are vulnerable to damage from bark-stripping over a much wider range of ages than from browsing. The limiting factors are initially the girth of the trunks, then

the thickness, hardness and smoothness of the bark (Ueckermann 1960; Wodarz 1962; Pellew 1968). Damage is heaviest in young trees, those aged between 7 and 20 years in many species (Rijcken 1965; Strandgaard 1967a; Vučković 1974), but between 18 and 30 years in Norway spruce because the lower branches protect the main stem at first (Ahlén 1965a; Pellew 1968); prickliness of the foliage, as in Sitka spruce, may give further protection. In several investigations the oldest trees stripped were aged 40 to 45 years (Lenz 1964; Ahlén 1965a; Strandgaard 1967a; Reijnders & Veen 1974). Schulz (1960) gives ages of vulnerability ranging from 3 to 15 years in poplar to 8 to 70 years in beech. In conifer plantations in Galloway, McIntyre (1975) found that the deer selected for trees with girth between 5 and 15 cm, damaging the larger trees in those stands with average girth less than 10 cm, and the smaller trees in other stands.

The bark taken comes most often from the sector of the trunks 0.75 to 1.25 m high, but occasionally from as low as 0.3 m and as high as 1.7 m (Ueckermann 1960; Rijcken 1965). In Yugoslavia Vučković (1974) reported damage up to 2.7 m above ground, but snow depths reach 1.45 m in the forest studied. Frequently a single wound is made, Wodarz (1962) giving averages of 23 cm for the length and 2 cm for the width. Sometimes damage is much more severe, particularly when the trunks are easily accessible; the deer may then remove almost all the bark within reach, girdling the trunks. Many workers recognise two types of bark-stripping: in summer when the sap is rising and the cambium active, bark is easily peeled from the stem, whereas in winter it is more difficult to remove and the deer gnaw it off with the incisor teeth (Daburon 1963; Rijcken 1965). Some trees are damaged mainly in summer e.g. beech, but conifers tend to attract most stripping in winter (Ueckermann 1960); in the English Lake District, there is a late-winter peak in damage (Pellew 1968). It has often been reported that changes to the structure of stands such as thinning and clearing are followed by more-intensive damage (e.g. Szederjei 1957), and it is generally considered that plantations are more vulnerable than natural woodlands (Rijcken 1965).

Marked differences exist between tree species in vulnerability to bark-stripping (Table 6). However, as Pellew (1968) demonstrates, simple ranking can mislead those wishing to manage deer or woodland, because of the effect of age on susceptibility. Thus, for stands between 20 and 30-years old at Grisedale in the Lake District, Norway spruce and Sitka spruce are the vulnerable species, although the latter is ranked least attractive overall. The ranking lists for bark-stripping and browsing by red deer are quite similar, alder, birch and Sitka spruce being of low preference, and ash, willow and *Pinus contorta* high. But silver fir suffers little from bark-stripping, and Norway spruce much, in contrast to their susceptibilities to browsing. Many other workers report Norway spruce to be the most-vulnerable species e.g. Ahlén (1965a) in Scandinavia, Borow-

ski & Kossak (1975) in Poland and Kurth (1964) in Switzerland, and damage to poplar is particularly serious in the Balkans (Vasić 1959a; Almășan 1966). So far little information on bark-stripping in the Scottish Highlands has been published, but Badenoch (1971) reported that Norway spruce and *Pinus contorta* were the species most-frequently attacked. McIntyre (1975) ascribed the high susceptibility of larch in Galloway (Table 6) to the presence of graminaceous vegetation attractive to deer in the field layer of its stands.

Many mammals eat bark on occasions, but damage from bark-stripping by sheep seems rare in Britain; it has been recorded in Galloway (McIntyre 1975), and in Aberdeenshire by the present authors. It is well known that cattle and horses strip bark, and extensive damage to rowan by cattle has recently been observed (Kinnaird, Welch & Cummins in prep.). Other trees were virtually ignored but certain species which might have been vulnerable were either too old or absent.

4.3.2.2 *Consequences.* When bark is stripped, a tree can suffer various injuries depending on the nature and extent of the wound. The whole stand is damaged if these losses exceed those occurring naturally and through thinning. Injuries include (1) growth reductions, in height or diameter, (2) timber defects, with discol-

oration and eccentricities resulting from mis-shapen trunks, swellings above the wound, ingrown bark, resin pockets and cup shakes, which cause loss of strength, and (3) pathogenic attacks, due to fungi or insects entering the tree through the wound (Žaruba & Šnajdr 1966; Holloway 1968; Pellew 1968; Knigge 1975). Sometimes death results, especially when the trees are girdled, and there is increased susceptibility to wind-blow and snapping.

Sharp differences of opinion exist on whether losses due to bark-stripping are serious, or whether they at most slightly delay felling; these views are reviewed by Rijcken (1965), Pellew (1968) and Stubbe (1970). Much depends on the species of tree involved: Stubbe considered beech and Norway spruce to be very vulnerable, and Douglas fir, silver fir and lime to be resistant, with variable reaction in pine and oak. It is generally agreed that Norway spruce is severely damaged. Žaruba & Šnajdr (1966) found that increment was sharply checked, but most damage arose from subsequent fungal rot. In Switzerland Kurth (1964) thought most stands, including Norway spruce, could be rehabilitated by judicious thinning. With Scots pine in Holland, Rijcken (1965) felt that stripping had no effect on growth, and though the quality of the timber was somewhat reduced, this damage was unimportant

Table 6. Some ranking orders of susceptibilities to bark-stripping by red deer

Author	Sablina (1959)	Müller (1965)	Ueckermann (1956 & 1960)	Strandgaard (1967a)	McIntyre (1975)	Pellew (1968)
Area	White Russia	East Germany	West Germany	Denmark	Galloway	NW. England
Highly-susceptible	Salix Fraxinus	Picea abies Fraxinus Pseudotsuga	Picea abies Fraxinus Salix Populus	Picea abies Pinus contorta Pinus mugo	Pinus contorta Pinus sylvestris	Pinus contorta Pinus sylvestris Picea abies
Moderately susceptible	Alnus incana Sorbus aucuparia Quercus Pinus sylvestris Picea abies Betula	Fagus Abies Pinus sylvestris Acer	Pseudotsuga Tilia Pinus sylvestris Fagus Larix Sorbus aucuparia Acer pseudo-platanus	Larix Pseudotsuga Picea sitchensis Abies	Larix Picea abies	Pseudotsuga Larix (Japanese) Larix decidua
Seldom affected	Tilia Carpinus	Quercus	Abies Quercus Alnus Betula		Picea sitchensis	Picea sitchensis*

* Cooper (1967), working in the same forest, reported that this species in some stands was considerably affected.

because of the use to which pine was put, whereas Soest & Stefels (1965) thought that its stem form was so impaired as to cause serious loss. In Denmark, Nannestad (1970) calculated that the 2,000 red deer caused an annual loss in Norway-spruce forests of between $\frac{1}{2}$ and 1 million Kroner, and at Fiunary, in western Scotland, Maxwell (1967) estimated that stripped pole-stage trees suffered a 40% reduction in volume increment. There is little doubt that bark-stripping can cause substantial losses in Britain, and even Sitka spruce is potentially susceptible to severe damage, often because more-preferred species are not available to the deer.

4.3.2.3 Causes. Much attention has been paid to determining why deer strip bark, so that appropriate remedial measures can more easily be developed. It now seems that no single cause can adequately account for all occurrences; indeed many causes have been suggested (Rijcken 1965; Prins 1968; Stubbe 1970; McIntyre 1972).

There is agreement that deer most often take bark for food, but opinions vary on whether trace elements, minerals, vitamins, alkaloids, roughage, energy-food substances, or even tannins, are the desired item. Several of these at least are present in useful amounts, making bark comparable to other high-quality foods (Wodsak & Ueckermann 1955; Wöhlbier & Lindner 1959; Ueckermann 1960). It has also been considered that bark is sometimes eaten as a source of water (König 1970a), or as a displacement activity caused by disturbance (Szederjei 1957; Chard 1966), or from boredom when the deer are given artificial foods and take little time to eat them (Bubenik & Lochman 1956), or as an antacid or tranquilant to reduce rumen disorders (Prins 1968), or as a marking mechanism by hinds to attract stags (Chard 1958). Rijcken (1965) felt that only certain individual deer stripped bark since it occurred in few of the rumen samples examined by himself, Jensen (1958) or Eygenraam (1960). Other studies, such as Dzięciołowski's (1970a), show, however, that this is by no means general. Furthermore there is evidence that once a few deer start to take bark, mimicry by others causes increasing incidence (Szederjei 1957; Cooper 1967).

It is also widely held that preferences for different barks may be due to variation in characteristics such as taste, ease of peeling, softness, digestibility and content of anti-microbial substances (Prins 1968). These factors are affected in turn by habitat and climate, for instance by the temperature and rainfall (Crombrugghe 1965a). It is becoming increasingly accepted (Prins 1968; Reijnders & Veen 1974) that winter bark-stripping is to obtain high-quality sugar-rich food, that spring bark-stripping is to obtain roughage, and that summer bark-stripping is due to various causes other than obtaining food because richer sources are then available.

4.3.3 Thrashing, fraying and other effects

Red deer also effect woodlands by grazing, trampling and dunging the field-layer; by rubbing trees; by fraying trees in removing velvet from the antlers; and by thrashing young trees with the antlers. In fraying, the bark of the main stem and branches is damaged, and in thrashing, branches are broken and leaves battered. The latter habit occurs particularly before the rut, and is thought to be induced partly as a show of strength and partly as a mark of presence, but to some extent it may simply be an outlet for excess energy (Nahlik 1959). Chard (1966) considered fraying by red deer to be less serious than by roe deer, and, although both fraying and thrashing can sometimes cause spectacular damage, especially on the edges of woods, they are generally regarded as unimportant, together with rubbing (Rijcken 1965; Pellew 1968).

The plant communities of the woodland floor are modified by the presence of deer much as those of open hill-land (see 4.2.1 and 4.2.2). Where the forest is dense *Calluna* is disadvantaged by the shading, and *Vaccinium myrtillus* and *V. vitis-idaea* take its place (Steven & Carlisle 1959). Under moderate shading herbivores apparently encourage this succession. As grazing pressure increases, the *Vaccinium* stands themselves tend towards grassy communities with *Deschampsia flexuosa* and luxuriant bryophytes, but the dynamics of these communities are not well understood. Where woodland is scarce and utilised for shelter, the grazing component of presence is relatively less important than trampling and dunging, thus producing a tendency towards poaching of the soil and local erosion, and perhaps also some enrichment.

4.3.4 Controlling impact in woodland

In devising measures to minimise damage, European workers have concentrated on (1) producing indices based on habitat characteristics by which acceptable stocking rates can be fixed, (2) developing reliable repellents, and (3) finding the most effective rates and techniques of artificial feeding. Fencing, although almost always used in Britain, is less popular in continental Europe and North America because of cost. In some areas, however, winter enclosures into which the deer are driven each year have been tried successfully (Ehrlich 1963; Jenkins & Reusz 1969). Forest management to provide alternative browse is recommended by Ueckermann (1960); it has been undertaken especially in the USA, but also in Europe and to some extent in Britain (Garthwaite 1967). A useful review on forest protection from red deer and other herbivores was made by Holloway (1968).

The site-evaluation method of Ueckermann (1951, 1957, 1960) uses the following characteristics: (1) % forest border with agricultural fields, (2) % grazing land within the forest, (3) tree-species proportions, and (4) geology, this last being given most emphasis. A site on sand, lacking fields or grazing land and bearing over

50% Norway spruce, would be assessed as capable of supporting just less than 1.5 red deer per 100 ha; below this density Ueckermann recommends that land should not be used for deer management. Müller (1965) included climate and the amount of grazing available in winter in his evaluation scheme, and the ratings for tree species were based mainly on their susceptibility to fungal attack. His lowest recommended density was 0.8 deer per 100 ha and he considered the minimum in Mottl's (1954) scheme, of 0.3 deer per 100 ha, to be too low for successful hunting. Maximum recommended stockings in the three schemes varied only between 2.5 and 2.7 deer per 100 ha, considerably lower than Scottish densities. However, the indices in their present form are not generally applicable, as discussed by Bubenik (1959) and Rijcken (1965); for instance Ueckermann's ranking does not change when the percentage of grazing land available rises above 21%. Local concentration of deer within the area evaluated also presents problems, and to apply the indices successfully needs reassessment of the site characteristics every ten years (Müller 1965), besides much effort in counting and culling.

Many ways of repelling deer from woodlands have been examined, including scaring with optical and acoustic devices (Nahlik 1959) and with smells of carnivores; Haaften (1965), for instance, hung up bags containing lion and tiger dung. The most useful deterrents to bark-stripping yet found are (1) painting or spraying the bark with chemicals, and (2) scarifying the bark with a metal roller. This induces resin flow, and makes the bark rough and difficult to peel (Ueckermann 1960; Strandgaard 1967a). If the scars are cut horizontally and carefully, neither the trees nor the timber are damaged. Fanta (1966) considered scarification to be cheaper, quicker and more effective than using chemical repellents, but potentially the latter is less demanding of labour if suitable long-lasting chemicals can be discovered.

Browsing and bark-stripping have been substantially reduced for up to a year, if not completely eliminated, by many different substances (Vasić 1959b; Ueckermann 1962; Crombrughe 1964a, 1965b; Strandgaard 1967a; Holloway 1968; Szukiel 1970, 1973). Efforts are being made to select repellents which are cheap, easily applied, long lasting and not inhibitory to growth (Holloway 1968; Paslawski 1970). Attention has turned to industrial waste-products for cheapness, and Szukiel (1973) considered raw gas-tar best, which has long been known to repel red deer (e.g. Jefferies 1894). The means of application tested include dipping the seedlings into the repellent before planting, and spraying by helicopter (Schreiber 1962). However, foresters in Britain consider that the use of repellents is still uneconomic on a plantation scale (Miss J.J. Rowe personal communication). Other means of mechanical protection such as polythene and wire-netting sleeves, and tying the side branches round the trunk (Ueckermann 1960), are very costly, although effective.

The provision of artificial foods to reduce damage to woodlands, is commonly practised in central and eastern Europe where, apart from the trees, little browse is available to the deer in winter. Large reductions in damage have been reported (Ueckermann 1960; Strandgaard 1967a; König 1970b), but much depends on the siting of the feeding points and the types of food used. Indeed some workers believe that giving abundant food can increase bark-stripping, either because roughage is needed to balance easily-digested high-quality food (Bubenik 1959; Veen 1973), or because they eat bark from 'boredom' (Bubenik & Lochman 1956; Szederjei 1957). In one of Szederjei's experiments deer spent far more time stripping bark when horse-chestnuts, a favourite food, were available at a central location than when they were scattered through the forest. It has also been considered that the failure to eliminate bark-stripping by artificial feeding is due to a lack of minerals or trace-elements, so attempts have been made to incorporate these in the food (Ueckermann 1964).

4.4 EFFECTS ON SOILS

The influence of red deer on soils has been largely disregarded in research studies and ecological thinking. In comparison, much has been written about the supposed adverse effects of other herbivores, particularly sheep (Darling 1955; Gorrie 1958; McVean & Lockie 1969). Although any herbivore modifying vegetation must influence the soil, no control measures are practised which have, as their primary objective, the reduction of deer impact on soils.

In grazed temperate-zone ecosystems, nutrients are lost by leaching and the removal of part of the secondary production. Losses of the latter kind due to deer must be small, because culling rates are low in comparison to those of livestock, and, in general, such losses are now considered relatively unimportant compared to input by rain (Crisp 1966; McVean & Lockie 1969). The plants producing litter most resistant to decay, and associated with leaching and podsolisation, include conifers and some broad-leaved trees, ericoid dwarf-shrubs and fibrous unpalatable monocotyledons (Dickinson & Pugh 1974; Heal & French 1974). In so far as deer allow *Callunetum* to replace *Agrostu-Festucetum* (see 4.2.1), they cause fertility decline (Gimingham 1971), but whether the losses are any greater than under sheep grazing, in which *Molinia* and *Nardus* often spread at the expense of *Calluna*, can only be decided from a full quantification of the extent and nature of the vegetation and soil changes in relation to the grazing received. In woodlands too, Sommer (1956) believed that deer, by browsing selectively on species producing readily-decomposed litter, would lower soil quality.

Herbivores have often been implicated in erosion, but red deer, because of their low densities, must cause little such damage except in highly vulnerable areas

like New Zealand. They construct 'bunkers' on slopes less often than sheep (Gorrie 1958; McVean & Lockie 1969), and do not persistently concentrate on favoured ground, unless attracted by supplementary feeding. But in one respect at least deer contribute to the erosion occurring in upland Britain; by wallowing in pools, a habit particularly frequent in summer when they occupy higher ground (Darling 1937), they seriously damage tracts of blanket bog with pool-and-hummock complexes. It is noteworthy that many of the best-preserved examples of this vegetation are in districts stocked in recent years by few or no deer (Ratcliffe (ed.) 1977).

4.5 EFFECTS OF THE HABITAT-MANAGEMENT PRACTICES ASSOCIATED WITH RED DEER

In Britain, the main management practice applied to land occupied by red deer is burning (Miller & Watson 1974); muirburn and deer are so associated that consideration of deer impact must involve an examination of burning effects. Other practices such as liming, fertilising, discing, reseeding and draining, occur chiefly on ground utilised by domestic stock and deer together. These practices can much affect the habitat.

Upland vegetation is burnt to provide palatable and nutritious young growth for herbivores, because their numbers are too few to consume the annual production of most plants, and a large biomass of unpalatable vegetation accumulates (Grant, Hunter & Cross 1963; Gimingham 1971; Miller & Watson 1974). The individual fires extend to several hectares in ground managed for red deer and sheep, burning taking place at regular intervals. Its effects on heather moors have been discussed by Gimingham (1971, 1972) and Miller & Watson (1974); less is known about other vegetation types. Important determinants are the frequency of burning (Kayll & Gimingham 1965; Mohamed & Gimingham 1970), season (Miller & Miles 1970) and the nature of the fire, this depending on weather conditions and the nature of the vegetation (Whittaker & Gimingham 1962). The speed of passage of the fire should allow rootstocks to survive, but sometimes *Calluna* and other ericaceous plants are killed, and can only re-establish from seed.

In the years following burning, various bryophytes, lichens, grasses, herbs and dwarf shrubs attain high cover until the *Calluna* canopy reforms, as Gimingham (1972) describes. Long-term trends in composition, occurring over several burning cycles, have not been measured, hence the speculative nature of the discussion on burning effects. Monocotyledonous hemi-cryptophytes such as *Agrostis*, *Carex*, *Eriophorum*, *Festuca*, *Molinia*, *Nardus*, and *Trichophorum* can tolerate severer fires, and severer grazing, than dwarf shrubs (Nicholson 1974), and would be expected to spread if *Calluna* declined under frequent burning. It is believed that such changes have occurred both on more-fertile, drier soils and wet acid peats; also that bracken

(*Pteridium aquilinum*) has been encouraged by excessive burning (Darling 1955; Gimingham 1972; Miller & Watson 1974). Gimingham (1971, 1972) considers that *Juniperus communis*, *Polypodium vulgare*, and some ericaceous species e.g. *Vaccinium vitis-idaea* are very susceptible to fire and have declined even more than *Calluna* and *Erica*. Furthermore, burning can occur so frequently that no saplings develop into trees, preventing succession to woodland.

In blanket bog in the western Highlands, the cover of *Calluna* has apparently decreased widely at the expense of *Eriophorum*, *Molinia* and *Trichophorum* (Darling 1955; McVean & Lockie 1969). Whether, as Nicholson (1974) believes, this is due to the high frequency of burning rather than the grazing pressures has not yet been proved. In Callunetum, succession after burning is strongly influenced by herbivores (Grant S.A. 1968); in an experimental study, *Calluna* increased more slowly under a high than a low intensity of sheep grazing (Grant & Hunter 1968). When grazing is absent heather develops into a tall open stand, but moderate grazing, by ruminants or mountain hares, encourages branching and lateral spread, perhaps helping *Calluna* to reassert its dominance more quickly (Gimingham 1949; Grant S.A. 1968).

There has been much concern that burning causes serious and irreversible decline in the quality of the habitat (Darling 1955; McVean & Lockie 1969). After a fire, the bared surfaces are vulnerable to sheet-erosion (Imeson 1971), and losses may be substantial when several years elapse before complete plant cover is restored. Gully erosion may occur on steeper slopes and sometimes, when fires have been too hot, the surface humus is destroyed (Gimingham 1972). Fire is also thought to make the humus less spongy, resulting in increased run-off in wet weather and quicker drying-out in drought (McVean & Lockie 1969); the skin of minute lichens that forms on the surface after a fire exacerbates these tendencies (Gimingham 1972). Long-term hydrological investigations are needed to quantify the effects. Nutrient loss in smoke and ash has received more attention (Elliot 1953; Allen 1964; Kenworthy 1964; Chapman 1967; Allen, Evans & Grimshaw 1969; Evans & Allen 1971). Input from rain seems sufficient to offset the losses in most elements, but perhaps not in nitrogen and phosphorus, especially when high-temperature fires occur. However, quantification is still inadequate for several of the pathways involved, including the uptake by plants and retention in the soil of nutrients from the ash, and also the release of nutrients from bed-rock and sub-soil.

Much research on fire ecology has been carried out throughout the world, but especially in North America. As yet many studies are descriptive, and of little relevance to British habitats. Although harmful consequences of burning are recognised, in many areas natural fires occur with worse results, hence prescribed burning is considered beneficial (Komarek 1969; Leege 1969; Kirsch & Kruse 1973).

The other management practices used in red-deer habitat have more-limited effects in space and time. Applications of fertiliser and lime raise plant and soil nutrient levels, but, unless the botanical composition changes so that a different type of litter accrues, the increased supply of nutrients is dissipated by leaching within a few years (Gimingham 1972). More-permanent changes are brought about by reseeding with grasses and clovers, but, again, if grazing intensities on improved areas are too low, ericaceous species invade and the swards gradually revert to their former composition. Heather has encroached on many of the shielings created by cultivation and the folding of livestock in the eighteenth and early nineteenth centuries in Highland glens, so that their presence can now be barely detected (Gaffney 1960). The effects of draining on the composition of the vegetation of wet peaty habitats are fairly negligible (McVean & Lockie 1969). Some hygrophilic species may be lost, but plants such as *Calluna* show increased growth where the water table is lowered along drains. Run-off characteristics also are modified, with sharper and greater peaks (Conway & Millar 1960) until the drains become choked; in areas of deep peat the drains can give rise to gully erosion (Mosley 1972).

A management practice of increasing importance in Britain is that of feeding the deer in winter (McLaren 1970; Paluchowski 1974). Normally only stags are fed, occasionally hinds also. The objectives are usually to improve the performance of the stags, so enhancing their trophy value, and to reduce mortality; sometimes easier culling, or the prevention of straying into farmland or forests, is the main motivation. As the practice affects deer distribution and feeding behaviour, it must affect also the vegetation and soil. Excessive local utilisation may reduce the availability of valuable food plants, and the animals may become dependent on the food provided and unwilling to range widely, as reported for wapiti by Murie (1951). In Scotland, McVean & Lockie (1969) drew attention to the lack of knowledge on the effects of supplementary feeding on the habitat, and Nicholson (1971) remarked, referring to Glen Feshie in the Central Highlands, that animal feeding does nothing to improve the range.

These latter comments are, however, more a reflection of current practice than potential. In many grazing systems at least, herbivores have to pay a penalty to sustain the productivity of desirable plants by consuming material that is less nutritious, otherwise this accumulates and the plants producing it spread, given equal reaction to equal intensity of grazing. Artificial feeding, by compensating for lower animal performance, gives managers an opportunity to select the stocking rates which produce and maintain the most-useful botanical characteristics and also a means of modifying the dispersion of the animals without the expense of fencing. Imaginative development in the British uplands of the equivalent of Szederjei's horse-chestnut feeding technique in Hungarian woodland

would be desirable.

Finally, some general remarks on supplementary feeding are appropriate. The different motivations of feeding in different countries must be stressed; thus, at present, its main purpose in North America is to reduce mortality (Dasmann 1971), in central and eastern Europe to reduce damage to woodlands (Ueckermann 1960), and in Scotland to improve stag trophy values (McLaren 1970). These motivations depend partly on ephemeral opinions of deer managers, but they also reflect differences in the habitats and the animals. Therefore caution is necessary in applying findings from other areas to Scotland (Jenkins & Reusz 1969), and regrettably no overall long-term evaluation has been attempted here. What knowledge is available suggests that feeding improves the condition and antler qualities of stags, but only certain dominant animals benefit when the food is not scattered widely (Lincoln *et al* 1970; Gossow 1971; Wiersema 1974); also that the distribution of deer can be altered to some extent (Dunnett 1974, 1975). On botanical impact and damage to woodland, we can still only speculate.

4.6 EFFECTS OF HABITAT MANAGEMENT AND RED DEER ON CONSERVATION

As rough grazings constitute by far the most extensive habitat for wildlife in Britain, and at least one third carry deer, with over 1 million ha in Scotland occupied exclusively, the consequences of deer presence and the associated management practices are of considerable importance for nature conservation. British upland vegetation contains relatively few species, many of which have very limited distribution (Rawes & Welch 1972); there are also few species of animals in comparison to other countries and other habitats (Darling 1947; Pearsall 1950; Steel & Woodroffe 1969; Nelson 1971). Many believe that impoverishment has occurred, and that the cause has been excessive grazing and burning (Pearsall 1950; Hart 1968). However, far fewer species have been lost from upland rough grazings than from other habitats in Britain in recent times (Hawksworth 1974), and most extinctions have resulted from causes such as clearance of forests and draining e.g. the wolf (*Canis lupus*) and *Trichophorum alpinum*. Climatic limitation also may explain the absence of some species (Conolly & Dahl 1970); others may not have returned to Britain after the last glaciation.

Stocking with red deer is widely held to have caused less impoverishment than sheep grazing (Raven & Walters 1956). Darling wrote in 1947: "The deer forest . . . tends to be a greater repository of wild life than the sheep farm and grouse moor . . . because it can allow and even encourage a greater variety of habitats". But judgement is complicated because of the different levels at which diversity is sensed; in the absence of long-term experiments, it is based on correlation between richness and the present occurrence of particular grazing regimes, ignoring the length of time

over which impact has accumulated. Deer, indeed, are adept at reaching tall-herb communities on crags, and they damage pool-complex bogs more than sheep (see 4.4), besides allowing coarser grasses and heaths to spread into herb-rich grasslands that would be closely grazed by sheep. In the Pennines, the occurrence of plant communities containing over 20 species of flowering plants per m² is associated with sheep grazing and small plant size (Grime 1973). The evaluation of floristic richness is based also on the totality of the flora, and the variability of vegetation on the scale of whole hillsides; judging between the impact of sheep

and deer in these respects is not yet possible.

The main alternative to grazing is afforestation. Its effects seem favourable on faunal, but not floral, diversity (Helliwell 1971; Steel & Woodroffe 1969). Even so, where woodland is absent or scarce, afforestation must add to the flora. Protecting the small remnant woodlands that occur in many Highland glens so that regeneration can occur, and withholding the use of fire from ground inaccessible to, or little used by, large herbivores so that chamaephytes and phanerophytes can develop, would also be beneficial (McVean & Lockie 1969).



Plate 7A

Central Highland glen with no regeneration of woodland and extensive areas of dwarf-shrub heath. The alluvial terraces are heavily grazed by red deer, and *Calluna* (dark patches) is being replaced by grassland (pale areas).

Plate 7B

Area of *Calluna* moorland in the eastern Highlands with light grazing pressure, being colonised by *Pinus sylvestris* (background) and *Betula* spp. (foreground).





Plate 8

Two examples of deer impact in woodland, upper showing naturally regenerating *Pinus sylvestris* with side-shoots browsed by red deer and the lower bark-stripping on *Picea abies*. Browsing of side branches is less serious than of leader shoots in commercial forestry. Amongst the conifers grown commercially in Scotland *Picea abies* and *Pinus contorta* tend to be the most susceptible to bark-stripping, and *Picea sitchensis* the least. Trees are vulnerable to this form of damage for a longer time than to browsing.



5. Red-deer populations: dynamics and performance

5.1 METHODS OF INVESTIGATION

5.1.1 Population size, density and composition

The literature on estimating large-mammal populations is extensive but Talbot (1970), Overton (1971), Seber (1973) and Caughley (1977) cover the main procedures (see Table 7) and their statistical backgrounds. The difficulties lie in applying these techniques to specific situations and assessing the reliability of estimates thus obtained.

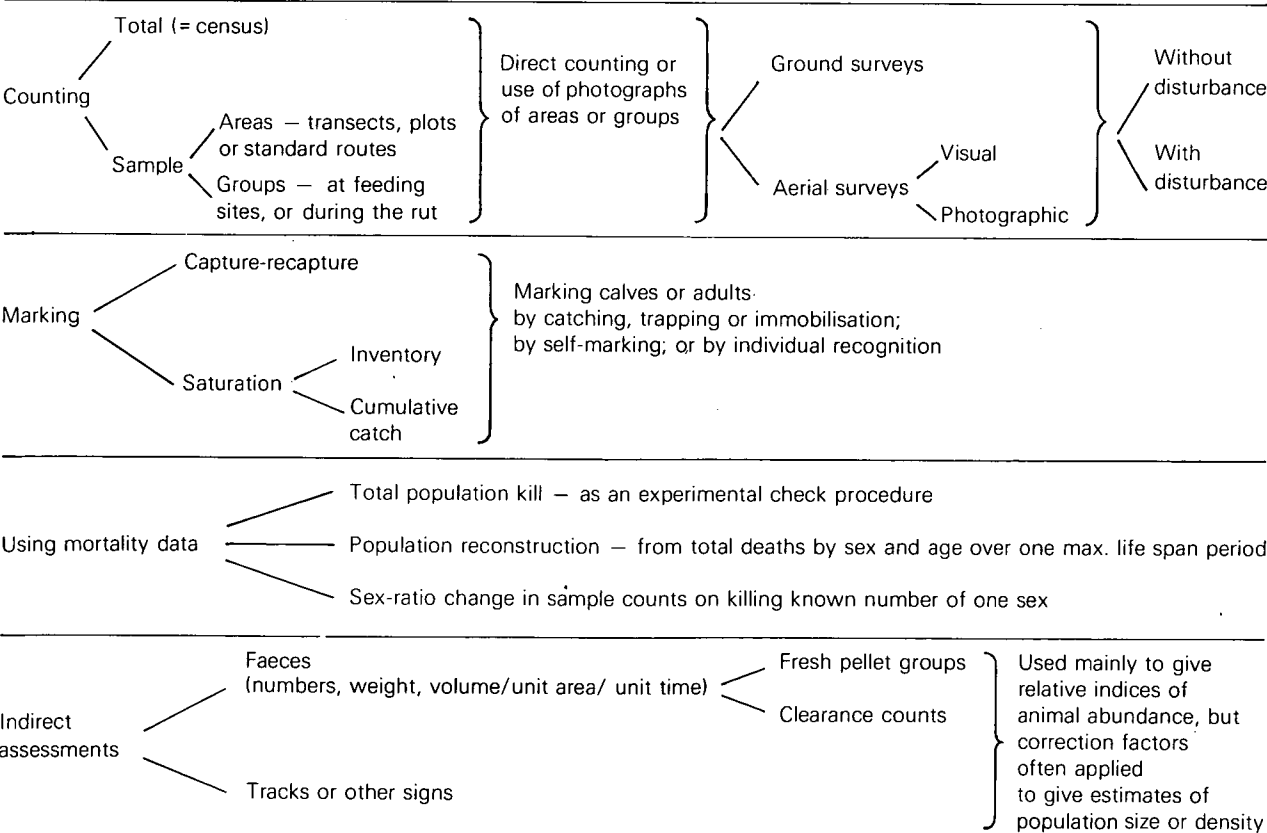
Choice of method depends first on the specific needs of the investigation, and the two extreme requirements are: (1) some form of density-index capable of detecting population differences or changes, and (2) information on population size and composition. The former is technically less demanding than the latter. Additional considerations include the habitat type, topography, and the distribution of animals. Populations of large mammals are more difficult to assess in woodlands than in open habitats, and in mountain or hill country than on flat terrain. Moreover, different approaches may be required for highly dispersed, compared with highly aggregated, populations.

In theory, there is no good reason why large terrestrial mammals cannot be counted accurately to achieve a census, or sample-counted to give estimates of population size or density; the distinction between 'deter-

mination' and 'estimation' is often misunderstood by practical managers. However, in practice, counting problems arise through concealment; animals may be camouflaged or obscured by habitat or topographic features, or they may actively avoid the observers. Animals widely dispersed are easy to miss, whilst large groups may be difficult to enumerate due to movements. Large areas of a continuous habitat-type present different counting problems, compared with smaller or more heterogenous areas.

Methods of 'drive-counting' are commonly applied to deer in woodland habitats. An area is systematically disturbed by a line of beaters spaced close enough to detect or disturb concealed animals, and the animals are either counted by the beaters as they break back through the line, or by other observers placed at strategic points around the area as the animals leave. However, Andersen (1953) showed that such methods can seriously under-count the population; a shoot-out of a roe-deer population in Denmark yielded three times as many deer (213) as the counts (70) on a 340 ha area. Andersen (1962) mentioned further examples when, in every case, shoot-outs yielded many more deer than were revealed by counts. Whilst Andersen's results have been quoted as examples of the difficulty or impossibility of counting deer in woodlands, we may

Table 7. Classification of main population-assessment procedures



question whether they apply to all deer in all woodland habitats. In Poland, for example, drive-counts have been used to check other less labour-intensive methods in woodlands (Pucek, Bobek, Łabudzki, Mitkowski, Morow & Tomek 1975). These woodlands, on relatively flat land, are broken into rectangular blocks by timber-extraction tracks. Counts are applied to a random selection of blocks, each requiring a large team of beaters with observers spaced along the tracks. Although not apparently tested by shoot-outs, these counts are regarded as censuses. This method would be impractical in the mountainous 'bush country' of New Zealand and in large areas of unbroken woodland.

Strip counts from aircraft, visually or by photography, have been used in some woodlands, either applying correction factors for concealed animals or by making the counts under conditions of low concealment. Kivilahti (1975) estimated that only 2-3% of the moose were not seen in aerial counts done in spring in Finland. Berdár (1974) described counts of big game, mainly red deer, in Hungarian deciduous woodlands in winter using a helicopter. Animal groups were easily detected and photographed through the bare branches and under-growth, against the snow background, at low altitude. These counts gave almost twice as many deer in each area as estimated by local game-keepers, but they would be less effective without snow or in coniferous woodland.

Two other methods, used widely for counting large herbivores in temperate woodlands, should be mentioned here, although we can find no published information on their accuracy. Deer and other large herbivores are often counted in winter, either at artificial feeding sites, or in natural, open, feeding areas. The accuracy of this method must depend partly on the behaviour of the animals, but also on local conditions e.g. the distribution of feeding sites or areas. Secondly, 'rutting' groups can be located from the 'roaring' of 'master' stags, and then be counted. However, deer not in such groups must be more difficult to find, and the rut itself, as seen on open ground, involves a good deal of irregular movements by the deer. At best, therefore, this method must give only a rough guide to the numbers and classes of deer present.

In open habitats, counting is easier, but less so in rugged mountainous terrain than on flat ground, and several methods have been described (Talbot 1970). Ground counts and aerial surveys have been applied to large mammals of the tundra and temperate plains of Europe, Asia and North America, and to various species on the African plains.

The first serious attempt to count red deer on Scottish hill-land was that by Evans (1890, also in Cameron 1923) on the island of Jura. Antlered deer (mature stags) were counted in autumn and antlerless deer (hinds and young) in spring over 11 years. The latter were classified into hinds, calves and young stags, thus giving approximate recruitment values i.e. surviv-

ing calves entering the population. From the numbers of deer shot each year, and counts of natural deaths, expected values were calculated for the adult population the following year. The estimates and counts of adult deer agreed reasonably well, suggesting that the counts were accurate. However, Lowe (1961, 1969) distinguished between accuracy and consistency in counting deer; the balance procedure was a test of consistency rather than accuracy, with possible compensatory errors in different factors.

Lowe (1969, 1971) studied the dynamics and responses to cropping of the red-deer population on the island of Rhum over 9 years. Counts of the deer were done in late winter and spring by 5 or 6 experienced deer-stalkers in 4-5 days. Apart from the data on shot animals, intensive searches were made to find all natural deaths, thus giving the total annual mortality by sex and age. These mortality data were used later to reconstruct the populations present during the first part of the study period (discussed further below), and the expected numbers of adult deer were then compared with the numbers counted. In brief, the totals agreed very well, indicating a high degree of counting accuracy. But the compositions of the counts and reconstructions differed, suggesting some misclassification of deer in the counts. About 10% of stags, presumably yearlings, were apparently misclassified as hinds, and there was evidence of misclassification between hinds and calves. However, some classes of red deer overlap in characteristics, and classification can never be exact, even at close range. Distinguishing between calves and hinds is especially difficult as the calves approach one year of age. The counting method used by the Red Deer Commission in Scotland (RDC Annual Report 1965; Stewart 1976) is similar to that of Lowe (1961, 1969), but the counting team is larger and equipped with radio-telephones. Most counts are done in the late winter and spring when the deer are on low ground. The deer are counted, mainly without disturbance, from higher ground, but they are flushed from concealment in rough terrain or woodland when necessary.

Shooting the whole population to check an estimate is rarely possible, and the best-known example is that of Andersen (1953, 1962), described above. The method used by Lowe (1969, 1971) on Rhum was essentially a natural kill-out spread over a long period. Records of the sexes and ages of all deer dying over the time of one maximum life-span gave the means for reconstructing the original population. But as Lowe showed, the original population could be reconstructed after a much shorter period by allowing for the likely survivors, a small source of error due to the small proportions of animals in the older age-classes. Discounting age-estimation error as a relatively minor factor, the only likely error was in the efficiency of the natural-mortality searches, and this was not measured. Although failure to find all natural deaths would reduce the apparent size of the reconstructed population, it could also affect the apparent age and sex composition; some classes of

deer would be more easily missed than others e.g. calves than hinds, and hinds than stags.

A further method using mortality data was partially examined by Holgate (1973), and it could be applicable where it is possible to record the total annual deaths e.g. woodland areas small enough to be searched thoroughly over the year for natural deaths. For a stationary population, the sum of ages in years of all those animals dying in one year gives the number of survivors. Departures from the stationary state (measured by index methods) could be allowed for if large enough or neglected if small enough. This method depends on unbiased post-mortem age estimation, a minor problem now with most deer species (see 5.1.2).

Capture-recapture methods appear attractive for some studies, owing to the relative ease of catching animals in some situations. Catching and marking animals may involve less concentrated manpower than, for example, drive-counts. Capture-recapture has been used reasonably successfully in studies of roe deer in Denmark by Andersen (1962) and Strandgaard (1967b, 1972). However, the underlying assumptions seldom, if ever, hold good for deer populations, and the confidence ranges are usually large. Whereas the latter are reduced by marking larger proportions of the animals, deer do not mix at random because of social factors, and the sampling of captures or recaptures could be biased.

The procedure of estimating populations from the sex-ratio change in sample counts after killing a known number of one sex has been tested on some deer in North America (Kelker 1940, 1944). It is mathematically similar to capture-recapture, and the assumptions (Seber 1973) seldom hold good for deer. Saturation marking, either to achieve a census, or to obtain a cumulative-catch estimate, has been little applied to deer. An exception may be at Cheddington, a wood in southern England, where a large proportion of the roe-deer population has been marked. Except for brief references by Cumming (1966) and Bramley (1970), detailed results have not yet been published.

Identifying animals from their individual features is analogous to identifying those marked artificially, and it seems potentially useful for censusing relatively small, easily-seen, local groups. This method has been applied to some large mammals e.g. feral goats in New Zealand (Rudge & Smit 1970) which show considerable individual variation in coat colour. It is also applied by some game-keepers to assess deer numbers in woodlands habitats; males are censused on the basis of individual antler characteristics. However, subjective judgement is involved, and the results are difficult to substantiate.

The various indirect methods of population assessment from animal products e.g. faeces (Riney 1957; Neff 1968), tracks, or signs, are potentially less costly and less labour-intensive than direct counts of animals. These methods are perhaps most useful in 'difficult' habitats e.g. thick woodlands, and in studies of relative distribution or habitat use. Whilst faecal methods,

based either on the occurrence of 'fresh' faeces or on the rate of accumulation in sample areas, are widely used at present, there are many problems of interpretation. Much remains to be investigated despite the large literature on the subject. Faeces may disappear at different rates depending on the site. Apart from the likely effects of variations of intake and digestibility on the rate of faecal output, it is not known for many herbivores whether they defaecate evenly over the ground used each day or at selected sites. In general, faecal techniques may be better adapted to detecting large differences in population density than to detecting small differences.

One method of estimating ungulate numbers from their tracks in snow, used widely in eastern Europe, has been criticised by Pucek *et al* (1975) as yielding lower and more variable estimates than drive-counts, and its logical basis may also be criticised. An index of density is said to be obtained from the difference between the number of tracks entering an area one day and those leaving the following day. However, the number of animals entering and leaving an area over a given period must depend on several factors, including the size of the area and the activity and numbers of the animals; an area of favourable habitat may have a resident population with little or no immigration/emigration. Similarly, density indices based on the numbers of tracks crossing transect lines in a day are difficult to interpret, as noted by Dzięciotowski (1976); he found significant correlations between the numbers of tracks and the results of drive-counts, with large mammals including red deer, in Polish forests. Since the number of tracks is also influenced by the activity of the animals, the method may be most useful for detecting population trends in single areas or for comparing numbers in similar habitats.

5.1.2 Age estimation

Although features associated with age in red deer are described in sporting and popular literature, individual experience seems the key factor in classifying live animals into age categories. For management purposes it is often sufficient to distinguish the young of the year from the older males and females. Overlap between classes makes more detailed classification less accurate (see Mitchell *et al* 1976).

Over the past 25 years there have been considerable advances in the post-mortem estimation of age in mammals, mainly using dental characteristics (Laws 1952; Sergeant 1967; Klevezal & Kleinenberg 1969; Taber 1971; Morris 1972). The main methods comprise those based on dental eruption and attrition, and those based on annual growth-layers in dental cement and dentine. The former could be influenced by the performance of the animals, and by their diet; high growth rates could cause early tooth development and hard food-materials could result in greater rates of tooth wear. Hence, the standards worked out for one popula-

tion may be less applicable to others. However, preliminary work on red deer from different parts of Scotland (Mitchell & Youngson 1969) suggested that rates of tooth replacement were relatively constant and that rates of eruption and wear were less variable between sources on cheek teeth than on incisor teeth. Moreover, there appeared to be no differences between the sexes, and the patterns of wear associated with age appeared similar to those published for German red deer (Raesfeld & Vorreyer 1964; Müller-Using 1971) as also noted by Lowe (1967) with red-deer material from Rhum. Nevertheless, considerable individual variation occurred, and age-estimates from tooth-wear may be correct on average, but often incorrect for individuals. Whilst the accuracy of this technique has not been fully tested with red deer, Lowe (1967), using known-age material from Rhum, found that tooth and mandible measurements gave correct age predictions with 88% of his material.

Methods based on growth layers in dental cement and dentine seem potentially more accurate than those based on relative changes in teeth. Eidmann (1932), working on German red deer, first showed the presence of annual secondary-dentine layers in the incisor pulp cavities, the thickest depositions being inside the crowns. The first layer was laid down at three years, but the earliest layers were later lost through dental attrition. Dentine layers have been found useful in many mammals (Laws 1952), but not generally in deer. The fact that secondary dentine grows by addition to the internal dentine surface, progressively reducing the size of the pulp cavity, makes the later layers narrower and less easy to count. Dental cement has the advantage of growing by addition to the external dentine surface apparently at a constant rate throughout life; cement layers tend to be more constant in thickness than dentine layers. Sergeant & Pimlott (1959), with moose, first showed the presence of cement layers, and their correlation with apparent age, in the incisors of cervids. The incisor-cement method was then found applicable to a large number of other mammals. The growth rate of dental cement varies according to tooth function and use; the highest growth rate occurs on the most heavily-used teeth. In effect, cement growth pushes the teeth out of their sockets at a similar rate to that of crown attrition, thus maintaining the contact between the upper and lower teeth. In single-root teeth, the cement forms a distinct 'boss' towards the root tip, whereas, in multi-root teeth, it often also forms a thick pad below the crown. In red deer, Mitchell (1963, 1967) found the cement pad on molar teeth easier to section and examine than the root cement. The lower first molar, the first permanent tooth to erupt, became the standard, as its number of layers gave the number of years exactly; later teeth required correction factors of +1 or +2 years.

Whilst tooth-layer methods have been validated for several species by using known-age material, the factors responsible for the layers are not yet fully under-

stood. Cell-rich ('summer') cement seems to be associated with the period of active growth, and cell-deficient ('winter') cement with the period of decline in body-weight and condition. Sometimes extra growth-layers are produced which can be recognised with practice e.g. rutting layers in some red-deer stags (Mitchell 1967). However, other factors may affect the growth of dentine and cement, making the recognition of annual layers less certain. For example, Lowe (1967) found less agreement between cement layers and age in known-age red-deer material from Rhum, than Mitchell (1967) with similar material from the Scottish mainland, perhaps because the annual growth cycle is less regular in the more oceanic climate on Rhum.

Further work is necessary to evaluate the factors affecting dentine and cement growth, and the relationships between layers and years of age in the same species in different environments. Nonetheless, in total, a useful range of post-mortem age-estimation methods now exist for red deer, and these make it possible to study growth, breeding and population structure using samples of populations.

5.1.3 Performance and condition

Measurements of the 'well-being' of individuals and populations are needed in management and in ecological studies of animal responses to environmental factors. 'Performance' and 'condition' are two useful but loosely-defined concepts of well-being. Performance relates to productivity of an individual or population, whereas condition relates to the state of an individual animal at a given time. Performance covers growth, breeding and survival, the proximal factors governing population turnover, whereas condition relates to the animal's life-expectancy (see Caughley 1971b). Condition is usually assessed in terms of the animal's metabolisable energy reserves, often simply in terms of crude fat. Condition is often used to cover both concepts as defined above, but the distinction is useful; condition is simply one aspect of performance.

Studying performance comprises finding: (1) the growth, breeding and survival potentials of the species; (2) how well the animal grows, breeds and survives under given circumstances; and (3) how growth, breeding and survival vary with environmental conditions. The techniques required vary depending on whether the animals can be (a) handled, experimentally treated and killed if necessary, (b) observed at a distance, or (c) sample-killed. Procedures applicable under (a) are those developed in agricultural research, and are covered adequately in agricultural literature e.g. Tribe (1964), Russel, Gunn & Doney (1968), Russel, Gunn, Skedd & Doney (1968). Observational assessments of performance on live animals (b) are particularly difficult. Riney (1960) assessed condition as an index of performance in wild red deer in New Zealand by scoring the relative thinness of individuals according to the prominence of their ribs and pelvic bones. This method is

most applicable during the least-favourable part of the year, when the variation in condition is greatest, but populations could differ markedly in performance with little difference in apparent condition. Capture (Taber & Cowan 1971) or immobilisation (Short & King 1964; Short & Spinage 1967) may help in the assessment of live wild animals, but little has been done up to now. The most practical method is (c), sample-killing with post-mortem assessments of age, body weight, reproductive state, and condition, although sampling is the most difficult aspect. Random sampling is rarely possible with deer; research often depends on animals killed for other purposes, with risks of bias and problems of estimation and inference.

The features commonly assessed as aspects of performance include body weight, skeletal size, condition, and reproductive status, related to age. In ruminants, the weight of the carcass less alimentary tract is more reliable than the weight of the complete animal as a measure of the real mass of live material, due to the relatively large size of the alimentary tract and the effects of variations in gut-fill. In red deer in Scotland, for example, the alimentary tract is 20-40% of the live-weight (Mitchell *et al* 1976). Many different measurements have been used as indices of skeletal size, the choice often depending on non-biological factors e.g. the market requirements of carcasses. These factors often also influence the choice of method of carcass-weight and condition assessment.

Chemical measurements of body-fat using minced-animal samples, as done in agricultural research, are rarely practical with large wild mammals. Instead, most condition assessments are indices based on different fat reserves, the chief ones being superficial body-fat, internal body-fat, especially that around the kidneys, and bone-marrow fat (Cheatum 1949; Bischoff 1954; Riney 1955; Batcheler & Clarke 1970; Caughley 1970, 1971b; Mitchell *et al* 1976). These reserves respond differently to changes in condition. In deer, superficial body-fat is present only when the animals are around maximum condition. Internal body-fat, especially perinephric fat, changes in parallel with body weight, but is less reliable as a condition index at the lower end of the scale. Perinephric fat is usually expressed as a kidney-fat-index: weight of fat or fat plus kidneys/weight of kidneys. The marrow fat in long-bones declines sharply when the animal is approaching very low body-weight and condition. Fat content and moisture content in bone marrow are inversely related, almost linearly, so the former can be estimated from the latter (Greer 1969). Greer (1968) also described a method of assessing fat content based on compressibility. However, it is often sufficient to distinguish between high-fat marrow (white and waxy) and low-fat marrow (red or pink and gelatinous). In red deer, white and waxy marrow contains 85-90% fat, whereas pink and gelatinous marrow contains 55% fat or less (Mitchell & Crisp *in prep.*). Some extremely low values (c. 1-5%) have been found in red deer dying of 'natural

causes' during late winter in Scotland.

As regards reproductive criteria, males are generally less useful than females. The only convenient comparative statistic in males is the age of puberty, but this is generally not sensitive enough for comparisons between populations. Killing hinds shortly after the rutting season can give information on their immediate breeding history (whether lactating) and current breeding status (whether pregnant). The reproductive features of hinds provide a useful range of comparative performance-statistics e.g. age of puberty, pregnancy rates in relation to age, mean calving-interval, and the proportions of sexually mature animals not breeding. The best reproductive index is the proportion of yearling (1½-year-old) hinds which are pregnant; this index approaches 100% in the highest-performance populations and 0% in the lowest. Similarly, the proportion of non-breeding sexually-mature hinds is a useful index of low performance.

5.2 PROPERTIES OF RED-DEER INDIVIDUALS AND POPULATIONS

5.2.1. Growth and development

The general pattern of growth and development in red deer has been well documented. Body weight, skeletal size, condition, and other anatomical features in relation to sex and age have been variously described in European red deer by Raesfeld & Vorreyer (1964), Lowe (1969, 1971), Mitchell (1969), Dzieciołowski (1970b), and Mitchell, Parish & Crisp (*in prep.*), and in North American wapiti by Murie (1951), Blood & Lovaas (1966), McCullough (1969), and Flook (1970). The annual cycles of growth in selected classes of Scottish red deer have been described by Mitchell *et al* (1976). Antler growth in red deer was investigated by Huxley (1926, 1931, 1932) as an example of allometry, by Lincoln *et al* (1970), Lincoln (1972) and Lincoln & Guinness (1973) in relation to reproductive physiology and behaviour, and by Lowe (1969, 1971) and Mitchell *et al* (*in prep.*) to describe and compare different populations in Scotland.

The pattern of body growth is typically mammalian; most active development is up to c. 5 years, with maximum body size and condition from 5 to 10 years, and a progressive decline above 10 years. Maximum body size and weight is attained at 6-8 years in hinds and 7-9 years in stags; maximum antler weight is achieved c. 2 years later. In hinds, maximum condition appears to be attained c. 2 years earlier than maximum body size or weight. Table 8 gives growth data from one Scottish population with relatively low performance.

As shown by studies of various other deer, for example *Odocoileus* spp. (Wood, Cowan & Nordan 1962), growth proceeds stepwise initially until maximum body size is attained, with the growth steps gradually becoming annual cycles in adult life, a pattern which must fit all large mammals in seasonally varying environments. Table 9 gives some key aspects of body

Table 8. Some physical characteristics of red deer at Glen Feshie, Inverness-shire: means of measurements of 2,286 animals (931 stags, 1,160 hinds & 195 calves) shot during autumn 1966-1973. Data from Mitchell *et al* (in prep.).

			Young					Prime					Old						
			Age classes (years)																
			C	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16 +
Stags		Carcase wt (kg)	26	38	49	67	74	82	82	85	85	84	83	83	77	82	74	80	69
		Jaw length (mm)	172	204	216	233	240	245	246	245	246	249	247	248	249	256	246	254	245
		K.F.I.	1.5	1.5	1.9	3.6	4.2	4.7	4.2	4.4	4.5	4.2	3.5	3.8	3.1	3.3	2.6	2.6	1.8
		Antlers wt (kg)	0	0.10	0.15	0.47	0.71	0.99	1.04	1.25	1.34	1.42	1.30	1.10	1.22	1.13	1.18	1.24	1.70
		N	99	45	12	33	100	151	150	133	95	59	45	43	36	11	12	3	3
Hinds	Non-lactating	Carcase wt (kg)	24	36	47	51	52	54	56	55	55	54	52	53	54	51	52	45	49
		K.F.I.	1.6	2.0	3.5	3.8	4.1	3.8	4.1	4.3	3.5	2.8	2.7	3.1	3.1	3.8	2.6	1.1	2.5
	Lactating	Carcase wt (kg)				44	46	48	48	47	46	47	44	46	44	44	46	40	48
		K.F.I.				1.9	1.8	1.9	1.9	1.8	1.7	1.6	1.5	1.5	1.4	1.5	1.3	1.3	1.3
	Total	Jaw length (mm)	169	201	215	221	226	229	231	232	235	232	234	237	235	237	239	236	232
		N	96	89	187	156	138	138	96	75	90	52	51	41	38	19	12	5	3

Notes: –
C = calf
K.F.I. = kidney-fat-index (wt. of kidneys plus perinephric fat/wt. of kidneys)
Carcase wt = wt of whole animal less alimentary tract (= c. 70% of live-weight)
N = sample size

Table 9. Weight and condition over the year in four classes of red deer: data from Mitchell *et al* (1976).

Carcase weight = weight of complete animal less alimentary tract. K.F.I. = Kidney-fat-index.

		Time of year						
Class	Item	early July	late Sept	late Oct.	late Nov.	late Feb.	late March	late April, early May
Stags (5-10 years)	Carcase weight (kg)	77	92	82	78	68	65	66
	K.F.I.	2.0	5.6	1.6	1.5	1.4	1.3	1.3
	N	10	14	13	12	12	11	9
Non-lactating hinds (5-10 years)	Carcase weight (kg)	52	55	61	62	56	57	56
	K.F.I.	1.7	4.0	3.7	4.7	3.4	2.7	1.3
	N	9	9	9	8	12	11	9
Lactating hinds (5-10 years)	Carcase weight (kg)	50	51	50	49	47	46	49
	K.F.I.	1.2	1.6	1.4	1.7	1.4	1.4	1.3
	N	11	11	10	16	10	11	10
Calves (sexes pooled)	Carcase weight (kg)	16	24	26	24	25	26	28
	K.F.I.	?	1.2	1.3	1.5	1.2	1.3	1.2
	N	9	10	12	14	12	11	11

weight and condition in selected classes of Scottish red deer at different times of year. These data indicate well-defined trends over the year in body weight and condition: growth cycles in the three classes of adults and a growth check over the winter in calves. Differences in carcase weight and condition between milk and yeld hinds of comparable age indicate the cumulative effects of pregnancy and lactation; in late November, after c. 6 months of lactation, milk hinds are 13 kg (20%) lighter than yeld hinds. In more-favourable environments the effects of pregnancy and lactation are lower; pregnancy rates are higher and yeld hinds are less common (see 5.2.2). Stags in Scotland show rapid losses of about 10 kg (11%) in carcase weight over the most active period of rutting, late September to late October, and losses of 14 kg (15%) over the whole rut, i.e. up to late November. The weight lost by stags during the rut may depend on the adult sex-ratio in the population. Comparing different populations in Germany, Raesfeld & Vorreyer (1964) concluded that weight losses in stags are greatest in populations where hinds outnumber stags, and least in those of equal sex-ratio.

Red deer vary in body size and antler development between different parts of their world range, and between different habitats, but detailed comparisons are difficult on account of the different measurements in existing publications. Hunting literature gives some indication of the variation (e.g. Bakkay, Kozma & Szücs 1971), but is highly biased towards the heaviest carcasses and antlers in mature stags. Much of the biological literature gives carcase weights based on local hunting traditions, often with the weighing method unspecified. The main features of the geographic variation in red deer are summarised in 2.2, but it should be noted that these comments cover major regional-variation; individual variation is much greater. Within the British Isles, few detailed comparisons are possible due to lack of comparable published data from the different habitats occupied by red deer. However, red deer in woodland areas especially deciduous woodlands, and deer-parks, clearly show higher rates of growth, higher adult weights, and larger antlers, than those on Scottish hill-land (Whitehead 1960, 1964; Mitchell 1969). The total range of variation may be similar to that found amongst European red deer generally, but this is an impression untested by reliable data.

5.2.2. Reproduction

Multiple conceptions and births are rare in most, if not all, red-deer populations (Murie 1951; Flerov 1952; Kittams 1953; Kröning & Vorreyer 1957; Flook 1970). Guinness & Fletcher (1971) give the only proven example of twin births in Scottish red deer. This example concerned a captive hind; fostering cannot be discounted in cases where two or more calves have been seen to suckle one hind in the wild. The frequency of twin embryos in pregnant hinds in Scotland was

recorded as less than 0.2% by Mitchell (1973a), whilst in pregnant yearling hinds in Germany and Austria Kröning & Vorreyer (1957) found 1.5% multiple pregnancies, including one example (0.1%) of triplets. The known case of twin births, and some of the twin embryos found in Scotland, were of mixed sexes, so at least some twin conceptions must be dizygotic.

Since red deer have single births, a well-defined breeding season, and a maximum of one calf/mature hind/year, the birth rate represents a useful index of performance. The maximum birth-rate is limited simply by the minimum age of puberty in hinds (Mitchell 1968, 1973a). Although mature hinds breed almost every year in some environments, reproductive output falls below this maximum in Scottish hinds because of the relatively late attainment of puberty and a post-pregnancy effect on condition, and hence on ovulation rate the following breeding season (Mitchell 1973a; Mitchell & Brown 1974). Polygamous mating makes it unlikely that the conception rate in natural populations is ever limited by stags not finding fertile hinds. Similarly, variation in the age of puberty in stags must have a negligible effect on the conception rate.

It has been shown in many mammals, for example farm livestock (Joubert 1963) and man (Frisch & McArthur 1974), that puberty and maintenance of fertility are influenced by growth-rate and condition; ability to breed seems to depend on a critical minimum body weight or level of condition. Evidence from shot animals (Mitchell 1973a; Mitchell & Brown 1974) and captive deer (Youngson 1970; Lincoln *et al* 1970) confirms this in red deer. In shot hinds, first breeders were heavier and in better condition than the sexually-immature animals of similar age, and amongst older deer fertile ones were heavier and fatter than non-fertile ones. Captive hinds reared experimentally on a supplemented diet on Rhum grew faster, and attained sexual maturity one year earlier (at 1½-years old), than wild hinds.

The extent to which puberty varies within and between populations of red-deer hinds is not known precisely. Daniel's (1963) report of sexual maturity in 5-month old calves in New Zealand is open to criticism because he interpreted large Graafian follicles as potential ovulations; *corpora lutea* or actual pregnancies would have been more acceptable criteria. Mitchell (1973a) referred to another report of sexual maturity in one male and one female calf in a Scottish deer-park. But these examples were exceptional; normally, the earliest that puberty is attained is 1 year 4 months (Kröning & Vorreyer 1957; Crombrugghe 1964b; Valentinčič 1960; Flook 1970). Whereas puberty may be attained by individual hinds over a wide age-range, the main year-classes are 1 to 3. Amongst populations studied in Scotland, the one showing the lowest mean age at puberty was at Glen Dye, an area with a reduced population density (c.16 deer/1,000 ha) due to high shooting pressure, where 64% of the yearlings were

pregnant (Staines 1970). Yearling pregnancies were rarer in other Scottish populations (Mitchell 1973a). Two higher-density areas (80-153 deer/1,000 ha) showed about 25% and 21% yearling pregnancies respectively. Glen Feshie, a higher-altitude area, with a high population density (131 deer/1,000 ha), showed no yearling pregnancies (Mitchell 1973a and Mitchell *et al* in prep.) most hinds becoming pregnant for the first time as 2-year-olds or 3-year-olds (Table 10). On Rhum (139 deer/1,000 ha), Lowe (1969) found no pregnant yearlings and no marked 2-year-old hinds with calves, in a 9-year study period. Elsewhere, Daniel (1963) mentioned that most first pregnancies occur in yearlings in New Zealand, as reported for English deer-parks (Mitchell 1969). Valentinčič (1960) reported that 30% of the yearlings were pregnant in lowland oak and beech forests, but none in alpine areas of Scots pine and beech forest or mountain pastures, in Yugoslavia. Kröning & Vorreyer (1957) and Crombrugghe (1964b) gave yearling pregnancy data for German, Austrian and Belgian red deer varying from 0 to 63%.

Ratios of calves to hinds in different red-deer populations are given in several publications, but these data are not all comparable in the seasons to which they apply. Those from shortly after the calving season represent birth-rates, but those from spring broadly indicate the levels of post-winter recruitment i.e. after neonatal and over-winter mortality. Since there are few measurements of mortality in calves, it is not possible to interpret the calf-to-hind ratios in detail. Riney (1956) found 28-70 calves/100 hinds in samples shot non-selectively at different times in several parts of New Zealand. From other non-selectively shot hinds in New Zealand, Caughley (1971b) calculated a female increment of 31/100 hinds i.e. a calving rate of 62/100 hinds. In counts of hinds and calves during late summer and autumn in Holland, Eygenraam (1962) found "not more than 45 calves/100 hinds" which he considered

low compared with the 64.8/100 given by Ueckermann (1960) as normal for West Germany. Eygenraam attributed this low value to the late attainment of puberty and the low breeding-rate in older hinds. Wegge (1974) compared an island population with a mainland population in Norway, and found calving rates of about 46-61/100 and 47-63/100 respectively. At Warnham Court, an English deer-park, c. 56 calves/100 hinds were found in annual captures of the whole population in autumn (Mitchell 1973a). North American wapiti show similar calving rates to most other red-deer populations (Murie 1951; Kittams 1953; Flook 1970). Red deer in Scotland seem to have uniformly lower rates of birth and post-winter recruitment than most of those elsewhere. Lowe (1971) estimated birth rates of 37.6-42.5 calves/100 hinds on Rhum, and Mitchell (1973a) 40-47 calves/100 hinds in three other areas. Deer counts in spring (data in Red Deer Commission Annual Reports 1961-1975) mostly suggest post-winter recruitment rates of 32-36 calves/100 hinds, although these estimates could be affected by misclassification to some extent.

Riney's results for New Zealand cover the range of variation found elsewhere. The highest value (70 calves/100 hinds) indicates a population in which the hinds become mature as yearlings, calve for the first time at 2 years, and breed successfully every year thereafter. The lowest value indicates the combined effects of late puberty and low breeding success in adults. Table 10 provides an example of the proximal causes of a low calving-rate in one population in Scotland; this calving rate was estimated at 40/100 (Mitchell 1973a; Mitchell *et al* in prep.). The earliest first-pregnancies were in 2- and 3-year-old hinds, the youngest lactating hinds being 3- and 4-years old. In sexually-mature adults, lactating hinds had a much lower pregnancy rate than non-lactating hinds, and old hinds were less fertile than prime hinds. It was further

Table 10. Fertility of red deer at Glen Feshie, Inverness-shire: data from Mitchell *et al* (in prep.).

		Table 10. Fertility of red deer at Glen Feshie, Inverness-shire: data from Mitchell <i>et al</i> (in prep.).																	
		Young					Prime						Old						
		Age classes (years)																	
		C	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16 +	
Stags	% fertile	0	77	100	100	100	100	100	100	100	100	100	100	100	100	100	—	100	
	N	19	30	10	18	22	31	26	21	16	12	8	4	5	2	1	0	1	
Hinds	Non-lactating	% fertile	0	0	63	83	93	93	96	100	85	84	87	94	89	67	60	0	0
		N	17	65	115	87	69	72	50	37	40	31	23	18	18	6	5	1	1
		% fertile						92						82					
		N						253						49					
	Lactating	% fertile				45	47	61	58	53	52	40	25	33	17	13	40	0	—
		N				11	19	18	19	19	21	10	16	15	7	8	5	2	0
		% fertile						50						24					
		N						103						37					

estimated that 30-40% of the sexually mature hinds failed to ovulate or conceive in a given year.

5.2.3 Age structure and life expectancy

The structure of the population by sex and age is fundamentally important to those managing red deer for some form of production (see 5.4). How far the population structure can be adjusted to suit particular forms of production is limited by natural life-expectancy in the different classes of animal. Life-expectancy is important as one aspect of the potential of the animal, but also as an index of its response to specific environmental conditions. It is useful to know the maximum life-span of the animal, and how life-expectancy varies by sex and age under different environmental conditions. Such information is usually summarised in the form of life-tables (Deevey 1947; Caughley 1966; Eberhardt 1971; Seber 1973).

Longitudinal studies of single cohorts to obtain 'dynamic' or 'age-specific' life-tables are rarely practical with large long-lived mammals, and most studies are done cross-sectionally to obtain 'time-specific' life-tables. The latter are based either on random samples of animals killed at a given time, or on the animals dying of all causes over one or more complete years. However, interpreting such data in terms of life-expectancy in relation to sex and age requires other information on the history and dynamic state of the population; fertility also influences the population structure (Coale 1957). The mathematical relationships between population structure, fertility and mortality have been well established in the life-table literature.

Mortality and population structure in red deer have been studied in Scotland by Lowe (1969, 1971), Staines (1970), Mitchell *et al* (1973), and Mitchell *et al* (in prep.), in New Zealand by Caughley (1971b), and in Canada by Flook (1970). Detailed comparison of these results is precluded by methodological differences and uncertainties about the histories of the populations. There have been no studies of completely-unshot populations of known demographic status, and the effects of competing kinds of mortality (shooting and natural) have not been investigated experimentally. Hence, the following comments are somewhat tentative.

The highest ages found in wild populations (c. 20 years) are similar to those in captivity (Mitchell 1970; Flook 1970), but extreme values are affected by sample size, being more likely to occur in large samples or large populations. One case cited by Evans (1890) of a wild Scottish hind possibly reaching 26 years seems credible in view of the quality of his other observations. Tooth attrition (Lowe 1969; Mitchell *et al* 1973) seems the limiting factor, since wild red deer do not survive long after losing their lower first-molar crowns; presumably this affects rumination efficiency. Tooth wear in Canadian wapiti is more rapid in males than females, giving a shorter life-span (Flook 1970), but this difference is not apparent in Scottish red deer (Mitchell unpubl.).

The pattern of natural mortality in Scottish red deer (Mitchell 1969; Lowe 1969; Mitchell *et al* 1973) suggests a typically mammalian form of natural life-table, although shooting must affect it to some extent. Natural mortality is relatively high during the first year, less so during the second, relatively low up to about 8 years, and increasingly high thereafter. Most natural mortality occurs in late winter and early spring (Lowe 1969; Mitchell 1973a; Mitchell *et al* 1973), and the rates are highest in those classes of deer showing lowest condition during autumn. Pre-natal mortality seems comparatively infrequent in Scottish red deer, and whilst early post-natal mortality may be relatively high there are few reliable estimates of this at present (Mitchell 1973a and unpubl.). Staines (1970), however, estimated losses of 29-44% between pregnancy and the first autumn of life in one population. Deer shot in Scotland have a different age composition from those dying of natural causes (Lowe 1969; Mitchell *et al* 1973); shooting tends to concentrate on the animals in the middle age-classes, extending to a lower age in hinds than in stags.

5.2.4 Sex-ratios in adults and recruits

The adult sex-ratio has some significance to those managing deer as a resource, quite different populations being required for sport compared with meat production (see 5.4). Less is known about the 'natural' adult sex-ratio in red-deer populations than about the broad patterns of mortality in relation to age, as discussed in 5.2.3. This is because unshot populations have not been studied in detail, and because the natural patterns of sex segregation, make sampling results difficult to interpret.

Parity between the sexes at birth occurs in most mammals, but small significant departures are often found in large samples. This feature has been best studied in man, and several factors seem important e.g. order and proximity of births, maternal nutrition, 'stress', and others (Colombo 1957). These factors seem to cause differential pre-natal mortality, the ratio at conception being in favour of males.

Miller (1932) found excess males (161 males:109 females) in embryos from Scottish hinds, but Lowe (1969) found excess females (108 males:137 females) in embryos from non-lactating hinds on Rhum. Moreover, Lowe found that the excess of females occurred in 5-8 year-old hinds (45 males:73 females) and that this was statistically significant. Caughley (1971c), however, disputed the latter conclusion. No patterns were apparent in the sex-ratios of embryos collected from Glen Feshie over a 9-year period (Mitchell *et al* in prep.). These comprised 226 males:237 females, with little variability between different classes of hinds. From these conflicting results it seems unlikely that there are large departures from parity, either in embryos generally, or in those from particular classes of hinds; normal sampling variability could explain the existing data.

The 'natural' adult sex-ratio is unlikely to be parity in a polygamous mammal, and most studies of red deer (Murie 1951; Lowe 1961, 1969, 1971; McCullough 1969; Flook 1970; Mitchell *et al.* 1973; Mitchell unpubl.) have revealed excesses of females, but rarely more than 2 females per male. Such results could be caused by differential natural mortality in the young, assuming parity at birth. In a Canadian wapiti population which was almost unshot, Flook (1970) found appreciably higher natural mortality in yearling males than females, and a lower maximum age in adult males than females. There were no indications of differential natural mortality amongst yearlings in Scotland (Mitchell *et al.* 1973; Mitchell *et al.* in prep.), and shooting cannot be discounted as the main influence on the adult sex-ratio. Traditionally, about twice as many stags as hinds were shot on deer-forests, though at present the numbers shot are equal (cf. data in Whitehead 1960 and Red Deer Commission Annual Reports 1974 and 1975). Also, stags are more likely than hinds to be shot as 'marauders' (Red Deer Commission Annual Reports 1961-1975; Grant P.C.H. 1968).

5.3 FACTORS AFFECTING POPULATION DYNAMICS AND PERFORMANCE

Whilst the various factors affecting the demography and productivity of red deer undoubtedly interact with each other, it is convenient to comment on them separately here. There is also much common ground between the factors affecting dispersion (chapter 3) and those affecting performance.

5.3.1 Genetic variability

Little is known about the performance potentials and other aspects of genotypic variation in *Cervus elaphus*. The belief, widely held amongst practical managers, that some kinds of red deer are 'better' than others in growth potential and antler formation, has not been tested adequately in controlled conditions. Experiments in deer-parks may have given some foundations for this belief, but much of the information is anecdotal or unpublished. Nonetheless, it would be unreasonable to expect no genetic differences between the indigenous populations of different regions. North American wapiti and European red deer retain their characteristic differences (Flerov 1952; Caughley 1971a) when reared in zoos or brought together in natural habitats by introductions, but there is no comparable information on the other 'races' within these groups. The low growth-rate and relatively small adult-size of Scottish red deer may be largely phenotypic; the animals are clearly not genetically incapable of better growth (see 5.3.2).

Morphological features and measurements have been used to compare red deer from different populations or geographical areas, implying that the differences are largely genotypic in origin, e.g. Lönneberg (1906), Ingebrigsten (1924, 1927), Beme (1957), Ahlén (1965b), Mystkowska (1966), Lowe (1972) and Lowe & Gardiner (1974). Whilst the deer in different areas or popula-

tions may well differ genetically, the inference does not necessarily follow from finding differences between allopatric populations.

Recent studies of 'blood types' in red deer are not open to this criticism, as the blood characteristics used have been adequately studied in other mammals and found to be genetically controlled. Lowe & McDougall (1961) and McDougall & Lowe (1968) found heterogeneity in serum β -globulins and transferrins within and between British red-deer populations, and Maughan & Williams (1967) found different haemoglobin types in British red deer. Work in progress includes studies at Göttingen University on blood proteins in German red-deer populations, and preliminary studies at Aberdeen University to find whether red deer can be classified on chromosome characteristics (personal communications). Whilst these techniques may help in the detection of genetic variability, it will be necessary to find what any differences mean in terms of the ecology of the animal e.g. whether there is heterogeneity in local populations due to introductions, and whether there are appreciable differences in the ways that deer of different 'provenances' respond to given environmental conditions.

5.3.2 Habitat influences

Information on the effects of the main habitat factors (nutrition and weather) on the performance and population dynamics of red deer is either fragmentary or anecdotal. Much of the work referred to in 5.2.1-5.2.3 concerns relationships between gross habitat-features and aspects of performance giving little basis for extrapolation and prediction, or it shows simply that red deer differ between one area and another. Red deer undoubtedly thrive better in woodlands and at low altitudes than in open habitats or at high altitudes. The relatively poor performance of Scottish red deer is generally attributed to their low-quality diet and the exposed conditions in which they live, and there is some evidence in favour of this, though population density is perhaps also important (see 5.3.3).

Grimble (1901) briefly mentioned that some calves, captured in Scotland and reared in an English deer-park, grew to much the same size as the other red deer in the park; these were much larger than the deer on Scottish deer-forests. Calves from Invermark deer-forest in Scotland were introduced to New Zealand where their progeny were said to rival the biggest European red deer (Donne 1924; Huxley 1931; Banwell 1968). Recent work on captive Scottish red deer (e.g. Youngson 1970; Arman 1971; Blaxter *et al.* 1974) has also shown that these deer grow faster, mature earlier, and achieve a larger adult size, on high-quality diets. Arman described one captive stag reared indoors which started antler growth at 5½ months, weighed 63 kg at 7 months, and had six-point antlers of 30 cm at 8 months. In wild Scottish red deer, antler growth starts several months later, and at 18 months the antlers are simple spikes usually less than 12 cm long. Wild calves

tend to be around 39 kg live-weight at 7 months (Mitchell *et al* 1976). Eleven female calves reared by Youngson on Rhum were fed partly on concentrates, and they reached higher live-weights (77 kg) than wild ones (46 kg) as yearlings. They also became sexually mature at 16-months old, at least one year earlier than usual (Lowe 1969, 1971).

The effects of weather and exposure on Scottish red deer have been studied mainly in relation to natural mortality. Using data from Rhum which has a wet, windy, oceanic climate, Lowe (1969), Anderson (1972) and Beddington (1973) found good correlations between rainfall, especially summer rainfall, and natural mortality the following winter. Natural mortality seemed to vary according to the condition of the animals in autumn which depended on the previous summer's rainfall. An exceptionally high mortality during early 1962 was associated with heavy rainfall throughout the previous year. In central and north-east Scotland, however, which have a more-continental climate, winter snow-fall may be the most important factor affecting natural mortality and other aspects of performance varying from year to year. Thus another example of heavy mortality (25% of the total deer, and 75% of the calves), occurring at Invermark (Fig. 1) during early 1963, was associated with prolonged snow-lie followed by cold dry easterly winds (Mitchell *et al* 1973). Moreover, the calving period in 1963 was two weeks later, and the calves were 20% lighter, than usual (Mitchell 1971); prolonged gestation and reduced birth-weight could have been consequences of the severe winter. In upper Deeside, Watson (1971) found a relationship between the period of antler casting, which tends to be related to the condition of the animals, and the winter weather; stags tended to cast their antlers late following winters with prolonged snow-lie and early in relatively snow-free winters.

5.3.3 Population density

Population density is usually considered the most important environmental factor affecting individual deer and hence their population properties, and it is the factor most easily changed by management. The concept of density-dependence covers two different processes which are often difficult to separate. Animals may affect each other directly through crowding and social stress, or indirectly through their competition for limited resources. This distinction may have little interest to practical managers; what matters is how the animals grow, breed and survive at different population densities.

There are several anecdotal or inadequately quantified accounts of changes in aspects of performance in red deer, mainly in carcase weight and antler development, associated with changes in population density. Grimble (1901) noted that carcase weights declined in many parts of Scotland during the nineteenth century when red deer were being actively encouraged to increase for sporting purposes. Raesfeld & Vorreyer (1964) quoted

examples from the hunting records of German state-owned forests during the early twentieth century showing that carcase and antler weights declined when red deer were allowed to increase, or that the quality of the deer improved when numbers were reduced. There are other accounts of downward trends in carcase weights and antler development as numbers increased after the establishment of red deer in New Zealand e.g. Huxley (1931), Banwell (1968), Harris (1973) and Clarke (1976). Challies (1973a, 1973b, 1974a, 1974b), however, has given a more-quantitative analysis of the effects of population density on growth, condition and fecundity in different populations in Westland forests, New Zealand. The deer in areas which they had recently colonised showed higher rates of growth and fecundity than those in areas long colonised. Furthermore, the deer in areas now subjected to heavy commercial hunting pressure were found to be improving in growth, condition and fecundity. Similarly, Buechner & Swanson (1955) reported increased recruitment following the reduction in one wapiti population in the USA, and Gross (1969) cited data showing the reverse trend in another population as numbers increased.

In Scotland, preliminary comparisons amongst different red-deer populations (Staines 1970; Mitchell 1973a and unpubl.) showed differences in performance broadly associated with density, though other factors could not be discounted e.g. altitude and vegetation. Staines found much higher rates of early growth and yearling pregnancy at Glen Dye (c.16 deer/1,000 ha) than Mitchell in a series of higher-density areas (c. 80-150 deer/1,000 ha). However, these areas differed in other ways, and there have been no detailed comparisons of red deer at appreciably different densities in similar habitats. In fact, the response to density in Scotland may be limited by homeostasis in the predominant vegetation types, forage being relatively abundant, but poor in quality, at most times of year.

Finally, work on various deer in the northern temperate zone (Klein 1968; Klein & Strandgaard 1972) points to 'starvation' as the main proximal cause of natural mortality, and hence as the main population regulating factor. Most of the exceptional 'die-offs' studied in various deer species in North America were associated with poor range conditions brought about by heavy utilisation (see 4.1.1).

5.3.4 Infectious diseases and parasites

Environmental influences on animal health include infectious diseases and parasites. Whilst there are many publications listing the parasites and diseases of red deer in North America and continental Europe, the details are irrelevant here. Work on red deer in Britain includes Dunn (1960, 1964, 1965a, 1965b, 1969), Latif & Adam (1973), McDiarmid (1967, 1968, 1969a, 1969b, 1970, 1972, 1974, 1975), McDiarmid & Matthews (1974), Rankin & McDiarmid (1969), Thompson (1967, 1968) and Twigg, Hughes & McDiarmid

(1973). Other information arising from the experimental deer-farm in Scotland is given by Blaxter *et al* (1974).

In general terms, the parasites (arthropods, nematodes, trematodes and cestodes) of red deer in Britain are better documented than the infectious diseases (bacterial, viral, protozoal, fungal etc.). Even so, the recent discovery of a new species of nematode in red deer on Rhum (Dunn 1964, 1965b) indicates that information on the occurrence of parasites is by no means complete. Most work has been concerned with the species found in red deer, with little attention to their effects, and with the role of red deer as a source of infection to domestic livestock. Finding diseases of agricultural concern in red deer could affect their status and management. 'Foot and mouth' disease and brucellosis have not yet been found in British deer, leptospirosis is apparently rare, and although louping-ill antibody has been reported, animals with clinical symptoms have not been seen. Avian TB has been found in Scottish red deer, but its distribution has not been investigated. Dunn (1969) lists 44 helminth parasites (36 nematodes, 5 cestodes and 3 trematodes) recorded in European red deer. Of these, 25 are primarily associated with domestic ruminants with 3 others occurring occasionally. Infestation levels in deer are generally low with little apparent effect on health or thriftiness.

Amongst the larger helminths in Scottish red deer, liver fluke (*Fasciola hepatica*) appears widespread but of little pathogenic significance (Mitchell unpubl.). Lung worms, presumably *Dictyocaulus* spp., have been found in red deer from several parts of Scotland, but there are no published data on their occurrence and effects. The two main tapeworm parasites (the adult stage of *Moniezia benedini* thought to be transmitted by an Oribatid mite, and the cysticercus stage of *Taenia hydatigena* a parasite of Carnivores) are comparatively rare, and insignificant as population factors. The tick *Ixodes ricinus*, is common on deer especially in the wetter, western parts of Scotland where it could have some effects on account of the high infestation levels. The other main arthropod parasites, the deer ked, (*Lipoptena cervi*), the deer warble maggot (*Hypoderma diana*), the deer nostril maggot (*Cephenomyia auribarbis*), and biting lice (*Damalina* spp.), are all specific to deer, and the only ones possibly having effects on performance are warble maggots and nostril maggots (Mitchell unpubl.).

In much popular literature, the diurnal movement of red deer between low ground and high ground in summer is attributed to irritation by insects. Whilst the diurnal and seasonal movements of deer do not correspond exactly with the cycles of abundance of any of the irritating insect species, red deer are clearly irritated by warble flies and nostril flies, as confirmed by our own observations. The head fly (*Hydrotaea irritans*) apparently causes severe irritation and reduced feeding-activity in stags at the experimental deer-farm in Scotland (Blaxter *et al* 1974).

Although parasites and infectious diseases seem relatively unimportant in their effects on Scottish red-deer populations on present knowledge, they have not been adequately investigated.

5.3.5 Natural predation

The control or elimination of large predatory mammals in much of Europe, and their absence from New Zealand, makes natural predation unimportant as a factor influencing most red-deer populations. Predator populations are less controlled in Eastern Europe, Asia, and in parts of North America, but little has been published on their effects on red deer. The results of severe control of predators on red deer in the Crimea were outlined by Kostyn (1970); antler 'quality' declined as deer numbers increased.

The effects of large predators on other deer species have been described briefly (e.g. Mech 1966), and apart from influencing population density (Klein 1965, 1970), the main types taken are apparently similar to those dying of other natural causes i.e. old, young and ailing individuals.

Eagles and foxes (*Vulpes vulpes*) have been considered potential predators of red-deer calves in Scotland. Whilst there are many reports of eagles attacking calves (e.g. Cooper 1969), and of finding calf material at eagle nest-sites and fox dens, the effects of these two predators must be quite small. Both species readily take carrion, a fact which could explain much of the material at nests or dens. Lowe (1969) estimated that eagles accounted for about 13% of the total calf-mortality on Rhum, but in this area eagles are comparatively abundant.

5.3.6 Supplementary feeding.

As far as we know, the effects of supplementary feeding (see 4.5) on performance in red deer have not been studied in detail, though there is anecdotal evidence on the effects of starting and stopping winter feeding on certain Scottish deer-forests. Carcase weights have been said to improve with the provision of winter food, and cessation of winter feeding in some areas has apparently resulted in high natural-mortality the following winter. However, Mutch *et al* (1976) found in one part of Scotland that only a small proportion of the stags got appreciable amounts of the food. Similarly, Wiersema (1974) found that only 43% of the stags resident at one feeding site competed for supplementary food, with 23% of the total stags getting 59% of the food i.e. c. 17% of their daily energy requirements. Some stags fed *ad lib* took c. 50% of their daily requirements. Thus, feeding at central points within stag areas is unlikely to have beneficial effects on the performance of the population as a whole. This practice may, in fact, have detrimental effects on the animals through crowding.

5.4 MANAGEMENT OF RED-DEER POPULATIONS: CONTROL AND CROPPING

As mentioned earlier (see 2.4), red deer may be regarded as pests or assets, or something between these extremes, depending on the dominant use of the land where they happen to be. As a pest they are controlled, excluded or eliminated, but as an asset they are usually cropped selectively, with attention to the composition of the population by sex and age.

5.4.1 Control of deer numbers

Elimination is usually done by intensive shooting, though poisons, mainly sodium monofluoroacetate ('compound 1080') are used to eliminate deer in some of the remoter protection forests in New Zealand (Daniel 1966; Barnett, Batcheler & Lambert 1970; Peters 1973). Reduction of numbers or local usage may be achieved by shooting, repellents or diversionary attractants, or fencing, or some combination of these.

The practicalities of control by shooting depend very much on the habitat; deer are less easily stalked in woodlands than on open land. Shooting in woodlands is done by driving the deer from cover or by using 'high seats'. The latter may be placed close to open areas used naturally by the deer, or special 'deer meadows' may be created by opening up woodland and encouraging attractive ground vegetation. There is a great deal of practical literature on these methods e.g. Nahlik (1959), Raesfeld & Vorreyer (1964) and Phillips & Mutch (1974).

5.4.2. Cropping red deer for sport or meat production

Before discussing the cropping of deer for different management objectives, some practical limitations must be considered. Whilst selection and killing are separate processes in the management of domestic livestock, they are inevitably combined in cropping wild deer. Capture for performance assessment and selection is hardly practical with wild deer, and the rifle is the main tool for manipulating and cropping free-ranging populations. Each kill involves decision-taking, and the main problem is to optimise the efficiency of selection and killing at a distance. Recommendations for selective shooting on theoretical grounds have to be related to the experience and practical skills of those doing the shooting. The difficulties of age estimation and performance assessment with live deer at a distance were mentioned earlier (5.1.2 and 5.1.3) and personal experience must be continually updated through comparing what is actually shot with the shooting requirements.

Selective shooting as the combined processes of controlling numbers, weeding-out poor stock, and adjusting the composition of the stock to suit the needs of trophy-oriented hunting, is the focal point of deer management in continental Europe, and there is legislation to ensure that set principles are followed. The theoretical population structures ('Hoffman pyramids') and culling plans to achieve them for trophy production given by Raesfeld & Vorreyer (1964) typify this

approach. The ideal population structure comprises an equal sex-ratio of adults but with a long age-structure of males (favouring the development of maximum individual quality) and a short age-structure of females (favouring high reproductive efficiency). Achieving and maintaining this structure involves killing older hinds, and poor-quality young stags, keeping the best stags until they reach maximum body size and antler development, and adjusting the relative cropping of stags and hinds to attain an equal sex-ratio in the population. By contrast, managing deer primarily for meat production requires a population structure with an excess of hinds, weighted towards the best breeders, and just sufficient mature stags to mate them, as in normal livestock farming.

Traditional red-deer cropping in Scotland, primarily for sport with venison as a by-product, was characterised by the paradoxical relationships of its management objectives and animal-husbandry principles, and by its inadequate biological basis. First, although red deer populations were maintained for stalking purposes, with mature stags as the sporting quarry, deer were under-cropped, especially hinds, and only mature stags were taken. This gave populations with an excess of hinds and a relatively young age-distribution of stags. Moreover, stags were often shot as marauders on agricultural land during winter, reinforcing the tendency towards adult sex-ratios in favour of hinds. The usual practice was to select large hinds in good condition without calves, partly because these were most suitable for marketing, and partly because failure to breed the previous year was thought to reflect poor individual reproductive performance. In fact, as shown by our own studies (Mitchell *et al* 1973; Mitchell *et al* in prep., and unpubl.) and those of Mutch *et al* (1976) a large proportion of these yeld hinds were 2 and 3-year-old potential first-breeders, and the others had high pregnancy rates. The most frequent age classes of stags were 5 and 6-year-olds, just below the ages of maximum body-weight and condition. Thus, whilst the stated policy on many deer-forests was to shoot mainly the poor-quality individuals, the age-compositions of the shot deer suggested otherwise.

Beddington (1973, 1975) and Beddington & Taylor (1973) used computer-modelling to examine the properties of red-deer populations in Scotland, and the likely outcomes of different harvesting strategies. They also examined the roles of economic and sociological factors in relation to management decisions on the kinds of population and production required. Whilst these theoretical treatments gave useful and realistic forecasts of directional influences, their magnitudes might be incorrect. Extrapolations beyond the original data need to be tested empirically e.g. effects of population density and adult sex-ratio on productivity. There are no data on the quantitative effects of population density on Scottish red deer comparable to those cited by Gross (1969) for wapiti in North America. Similarly, the calculated changes of biomass production associated with those in adult sex-ratio are based on several

assumptions which have yet to be justified.

Existing cropping theories mostly fail to consider adequately the possible genetic consequences of 'non-natural selection', except in the restricted case of antler formation in stags. What the sportsman or venison market requires, or what the population can be made to yield by appropriate cropping, may conflict with maintaining population 'fitness' to local conditions (Mitchell 1968). 'Non-natural' mortality must impose its own selective pressure, and this kind of influence has not been considered adequately. Maintaining genetic fitness requires the elimination of those deer likely to die naturally during winter i.e. poor or ailing individuals amongst the younger and older age classes (see 5.2.3). There is no reason why this policy should conflict with the other objectives of cropping, but the market has to be content with a leaner average product and a wider variety of deer. The main problems in cropping free-ranging deer are those of identifying 'thinnings' from 'final crop' in a mobile population of mixed age-classes. An alternative approach would be random shooting, as this would impose no genetic selection pressure on the population. However, random shooting is not acceptable to those managing deer for sport or meat-production (see Mutch *et al* 1976),

and it gives a lower total yield than selective shooting.

The maximum sustainable rate of cropping for red deer, as indicated by calving data (see 5.2.2), must be about 35% of adults annually in the highest-performance populations, assuming an equal sex-ratio of adults. In fact, Raesfeld & Vorreyer (1964) recommend cropping about one-third of the adults annually in German forest populations, and this is the rate adopted for most populations in forests in continental Europe. Here, the population densities are low, the animals are given supplementary food in winter, calving is high, and natural mortality is apparently insignificant. Recruitment data for Scottish populations suggest a potential cropping rate of 16% of adults, or slightly more, and a 'one-sixth cull' has been recommended by the Red Deer Commission (Annual Reports 1961-1975) as a useful starting point; this is much above the traditional level. The differences in biomass production between forest populations in continental Europe and those on Scottish hill-land are much greater than the numerical cropping rates would suggest since individual growth-rates are also higher. Finally, as indicated above, manipulating the adult sex-ratio in favour of hinds must increase the productivity of a population, but this practice has not been investigated experimentally.



Plate 9

Hind groups on snow in winter, the ideal conditions and season for counting deer. From late autumn to spring the deer occupy the lower parts of their range where they are easiest to see and classify. In winter also, the deer are least likely to move far when disturbed, but for counting in rough terrain or woodland they must be flushed from concealment.



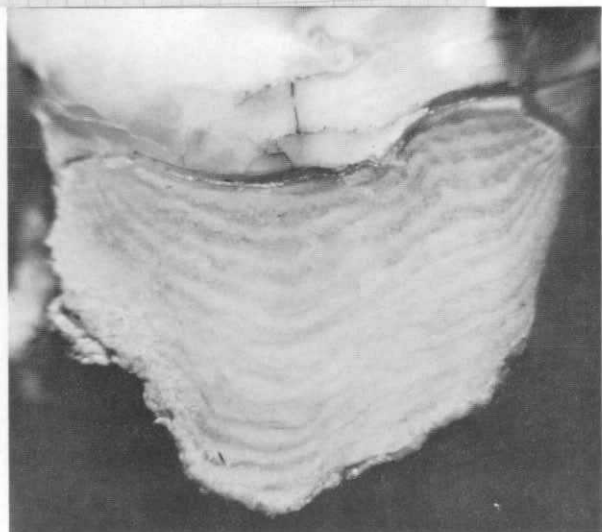
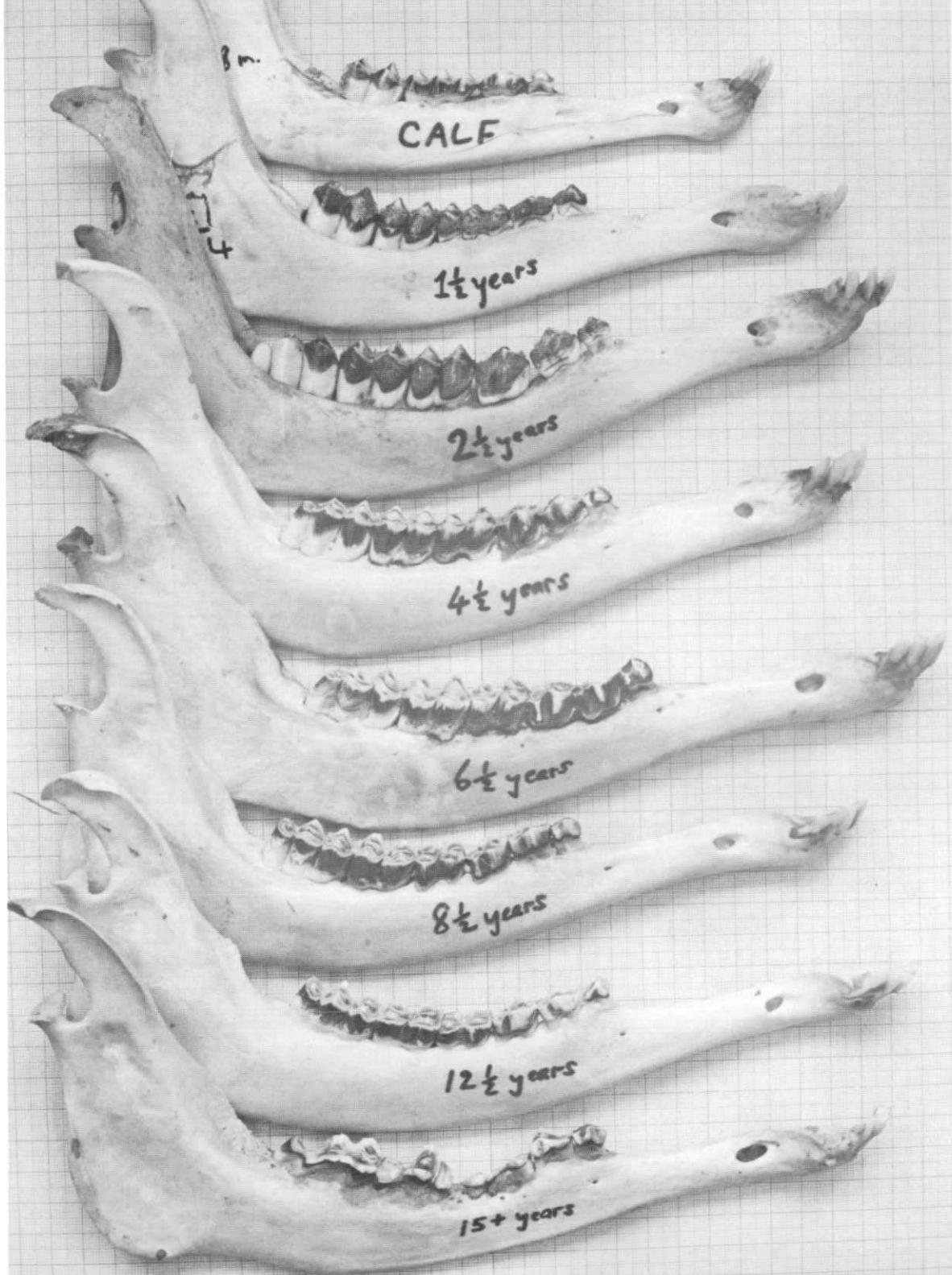


Plate 10

Dental features indicating age. Upper shows the eruption and attrition of mandibular teeth. Lower shows growth layers in the pad of dental cement below the crown on a lower first-molar tooth (magnification x12); the number of white layers gives the age in years.



Plate 11

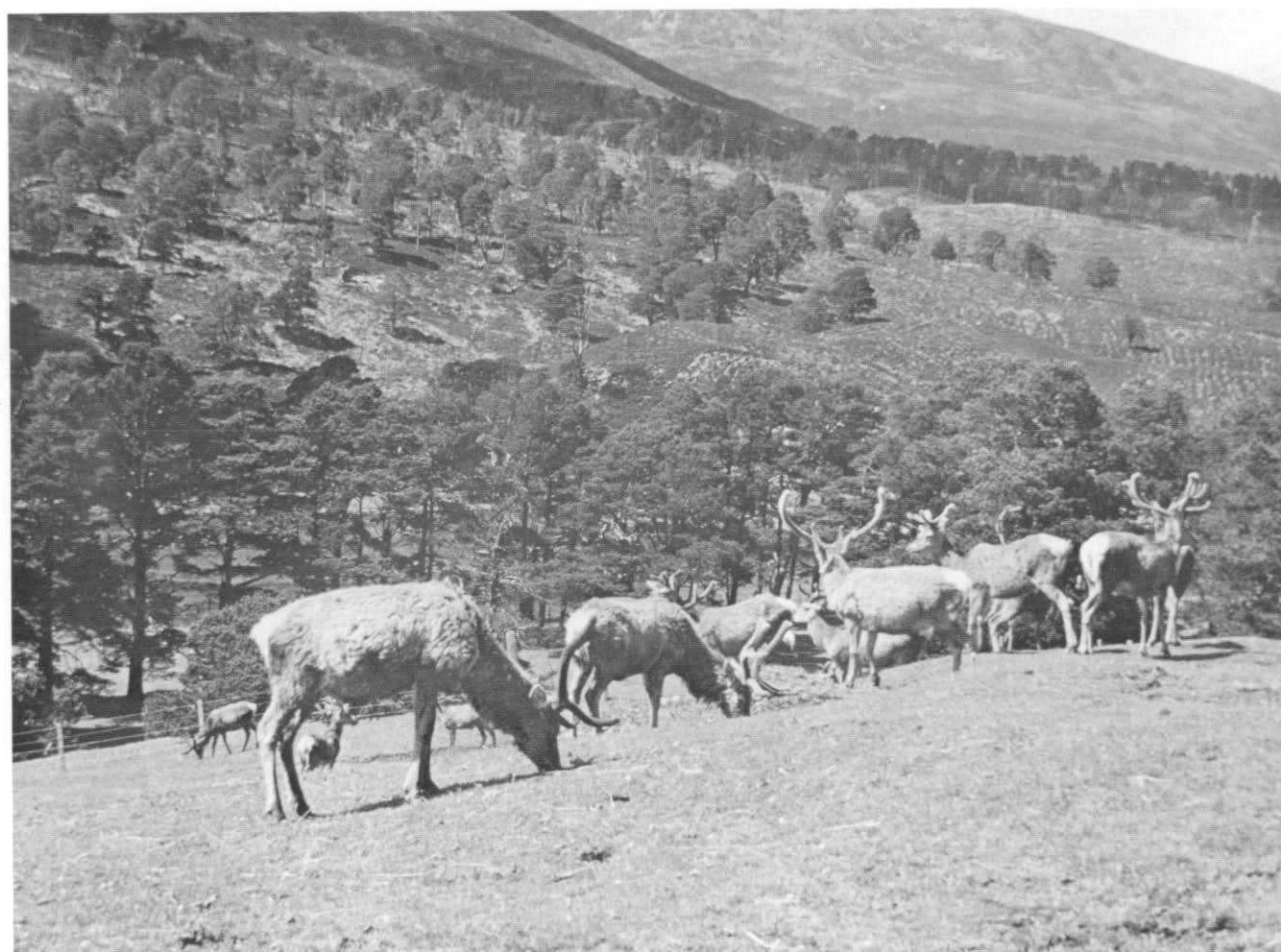
Natural deaths in late winter: a 9-month-old calf (upper) and an old stag (lower), both being extremely emaciated with little discernible body-fat and low marrow-fat. Natural deaths typically comprise the young and old of both sexes. Animals dying naturally have well-filled rumens, suggesting that they were able to obtain food of some sort until shortly before death. Most hinds found dead in winter are not pregnant, indicating that they were in poor condition the previous autumn.





Plate 12

June on Scottish deer-forest land, a time of abundant fresh forage. A 2-day-old calf (upper), newly ear-tagged for research purposes, in a typical situation where it was left by its mother between feeds. Calves spend much of their time lying concealed during their first two weeks of life. Stags (lower) at a supplementary-feeding site. In the background is a remnant of natural Caledonian Scots-pine forest, now replanted. Fencing is necessary to exclude deer until the trees have grown beyond their vulnerable stage or until the ratio of animals to saplings is reduced.



6. Discussion and recommendations

In discussing the material contained in the previous chapters, we first make some general remarks about the red deer. Then, in assessing what is known about the animal, and considering the problems it is causing in Scotland, we also make recommendations on research priorities. Lastly, from the knowledge now obtained, we comment on some aspects of current management.

6.1 APPRAISAL OF PRESENT KNOWLEDGE

The red deer is a successful and versatile animal, having a wide natural distribution, mainly in the temperate zone. Like other cervids, it is less tolerant of hot, extremely cold, and arid climates than some of the horn-bearing bovids. It is highly mobile, but, in mixed-grazing systems with domesticated stock, it occupies auxiliary rather than dominant positions. Being a ruminant, it can utilise a wide variety of food and survive on low-quality forage, because digestion can be comparatively thorough and intake large. In poor-quality environments, population turnover may be reduced through delayed puberty, biennial conception and slower body growth, allowing it to persist in relatively high numbers. However, red deer cannot respond quickly in numbers and biomass to favourable habitat changes, at best increasing by about one third of their numbers in a year, while some other wild ruminants, for instance roe and white-tailed deer, have the potential to double in number.

Red deer in Scotland are at the northern edge of their natural range, and are not perhaps such hardy animals as commonly thought, having relatively thin coats and little superficial body-fat. Compared to domesticated sheep, they have higher maintenance requirements, partly because of their poorer insulation, but also because of their greater activity. Indeed the ability of red deer to travel long distances to obtain favourable conditions and food is a major adaptation enabling them to overcome the difficulties of their environment.

Red deer are less selective for food than sheep and apparently less capable of digesting some forages; this, coupled with their higher maintenance requirements, means that they need a higher food intake per unit of body weight. Thus they have a different feeding strategy to sheep, the higher intake offsetting the lower selectivity. Also, although individual red deer gain weight somewhat faster than sheep, populations of sheep appear more efficient at converting their food into secondary production, due, at least in part, to management and selective breeding. Furthermore, sheep can maintain the vegetation on the better soils in a condition more favourable to themselves. Consequently, the output of sheep on a little-managed, high-level grazing in the north of England (Rawes & Welch 1969) is at least as great as so far obtained in the fairly intensively managed deer farm at Glensauigh in north-east Scotland (Blaxter *et al* 1974). However, insufficient information is available to permit firm conclusions on which herbivores are best for particular types of upland habitat in Britain, considering both

yield and impact.

To produce a predictive model of the ecosystem centred on red deer, useful to management and capable of discriminating between the major and minor variables, we need quantitative information both on the component factors and their functional relationships. The main features of the system are illustrated in Fig. 3, and we examine these in turn, stating what is known in the Scottish context, and evaluating to what extent changes can be initiated, controlled or predicted.

Habitat selection, expressed in the density, dispersion and home range of the deer, is clearly a key process, by which the performance of the animals is influenced by the vegetation, and by which the animals at the same time affect the vegetation. The other processes, limitations and influences take effect only after habitat selection has occurred.

The dispersion patterns of the deer result from both positive choice of good conditions and avoidance of difficult conditions. They are influenced by the spatial distribution of ground affording such conditions in relation to the more-neutral remainder of the range, the social behaviour of the deer, competition from other herbivores, and disturbance from man, which often excludes deer from habitat they would otherwise occupy. Within deer ranges in Scotland, densities vary from virtually zero on inhospitable ground to around 2 animals per ha on some lower areas offering good feeding or shelter. There is often an approximately twenty-fold increase on favoured sites over the overall stocking density of 1 deer per 10 ha. Food seems to be the most important determinant although, in the short term, climatic and social factors are at least equally important. However, much more work is required before we can predict dispersion and usage at individual sites, knowing the overall number of animals and the magnitudes of the modifying factors. Thus we have as yet little control over habitat selection by deer.

To relate knowledge on habitat selection to impact requires information on food selection and grazing intensity; additionally, information on home range and food quality is needed to relate habitat selection to performance. Little is yet known on the extent of home ranges or the elements of habitat they contain habitually or obligately, for different classes of red deer in Scotland. Where feeding grounds are extensive and juxtaposed with shelter, home ranges may be around 400 ha for hinds and 800 ha for stags, but elsewhere they may be much greater or even smaller. In this and many other attributes, the red deer is clearly variable, and misleading conclusions can result from studies in single areas.

Present knowledge on which plant species and which parts of plants are selected from what is on offer is also poor. Botanical analyses of rumen contents show that, in Scotland, a wide range of material is taken including browse, that certain species are consistently preferred and others neglected, and that there is considerable variation between seasons and between differ-

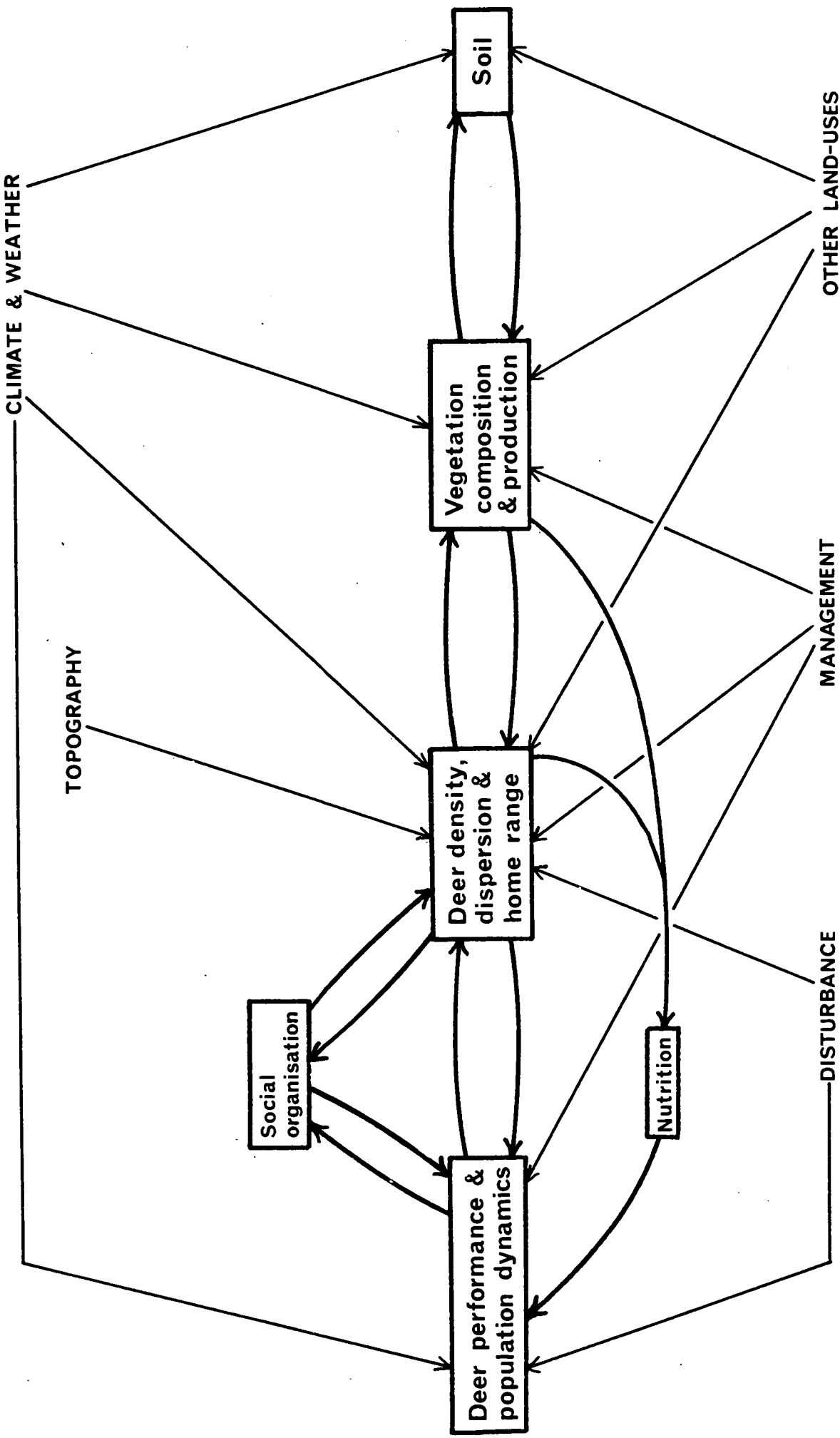


Fig. 3 Relationships amongst the principal ecological and management factors involving red deer.

ent areas. However, rumen analysis gives only a rough idea of selection unless it is known where the animals ranged and what was available there. Only rarely have such data been obtained, and further work in different parts of Scotland is required to produce an adequate general description of food selection. For this purpose there is an obvious need to categorise plant-community types in terms related to their values to the deer. Studies are also necessary to confirm the suspected variation in grazing intensity between different vegetation types and times of day.

Interpreting data on intake needs information on the nutritional values of the forage and the nutritional requirements of the deer. At present, we have to estimate the latter mostly from work on North American species and domestic stock, whilst the plants for which analyses are available tend to be those utilised by sheep and cattle. A comparison of the requirements and digestive physiology of red deer and sheep would be profitable, so that the large amount of information on hill sheep could be related to the deer. There is also a need to bridge the gap between indoor and field studies, because the energy and dietary requirements of the deer, and the way they fulfil them, vary so much in different circumstances. It is, however, clear that the quality of the diet under typical Scottish hill conditions falls well short of the optimal, so that performance is much inferior to that obtained in some woodland habitats, deer-parks, and captivity.

Little objective information is available on whether the factors which modify dispersion and food selection have significant effects on impact and performance. Disturbance and social behaviour are easy to recognise, but not easy to evaluate over longer periods; thus stags are clearly dominant to hinds in direct encounters, but this does not explain the patterns of segregation. Also, although there is evidence that the number of animals utilising particular sites or foods is sometimes restricted by social factors, the consequences of the existence of hierarchies and groups of particular size are unknown, either for individual or whole-herd performance. The interactions between food availability and weather conditions, especially shelter, need special study, not only for the objective of explaining the total usage, but also because knowledge on requirements at critical times of the year would guide management decisions on the most-valuable types of vegetation to develop.

In comparison to the dearth of knowledge on habitat-herbivore interactions, far more information is available on population dynamics and performance. In Scotland, deer attain maximum body size at about 8 years, with very few individuals living beyond 15 years. Natural mortality is high in calves and becomes increasingly heavy beyond 8 years, single births are normal, conception is frequently biennial, and puberty is usually reached at 2 or 3 years of age. It has been shown that variations in conception rates, the age of puberty and in mortality are related to body weight and condition, and

can be predicted quite closely. However, the effects of animal density and habitat quality on the various aspects of performance are not well established. These effects are determined by the factors previously discussed, particularly home range, habitat selection, food selection and food quality, but it might be expected that a direct relationship of predictive value between density, habitat quality and performance could be obtained.

As an example of how far we have progressed towards determining such functional relationships, we present some data from eight Scottish populations (Fig. 4). Analysis suggests a significant relationship between one aspect of performance (yearling-pregnancy rate) and stocking density, the latter being expressed for statistical convenience as its inverse. However, habitat quality was not quantified and the populations were in areas differing in altitude, habitat type and management. Even with a measure of habitat quality, multifactorial analysis would have been unwise with so few data available. Thus, to substantiate the apparent relationship more-extensive studies are required on a wider range of population densities and with more-adequate environmental assessments.

The impact of red deer on plant communities has been little studied, but dwarf-shrubs seem to be encouraged at the expense of grasses because the deer do not utilise grasslands so intensively as cattle and sheep. Further work is required to produce a generalised model for the British uplands as a whole of the variations in the herbivore densities that cause successions between the main plant communities; there is as yet insufficient evidence to single out any herbivore as having the most deleterious impact. Long-term trends in soil fertility consequent on the presence of the different plant communities are imperfectly understood, and the effects of burning need to be disentangled from those of the animals. At present, with our lack of knowledge on habitat selection, the impact of deer can be controlled only by altering their overall numbers.

The most important way in which deer influence British vegetation is by preventing woodland regeneration or succession to woodland. But tree establishment in the presence of deer formerly, and in some areas now, gives grounds for the expectation that woodlands could become once more a viable element in a habitat comprising a mixture of vegetation types if browsing pressure were reduced, or the number of saplings increased. We examine this in some detail as an illustration of the many and diverse factors that often have to be measured before predictive ability is attained (Table 11). Reliable estimates are needed of (1) the intake of browse by deer, its limits, and how far these can be modified e.g. by artificial provision of browse, (2) the dispersion and densities of saplings around woodlands of different types and spatial patterns, and (3) the growth rates and reactions of saplings to browsing. Also, at least five major assumptions need to

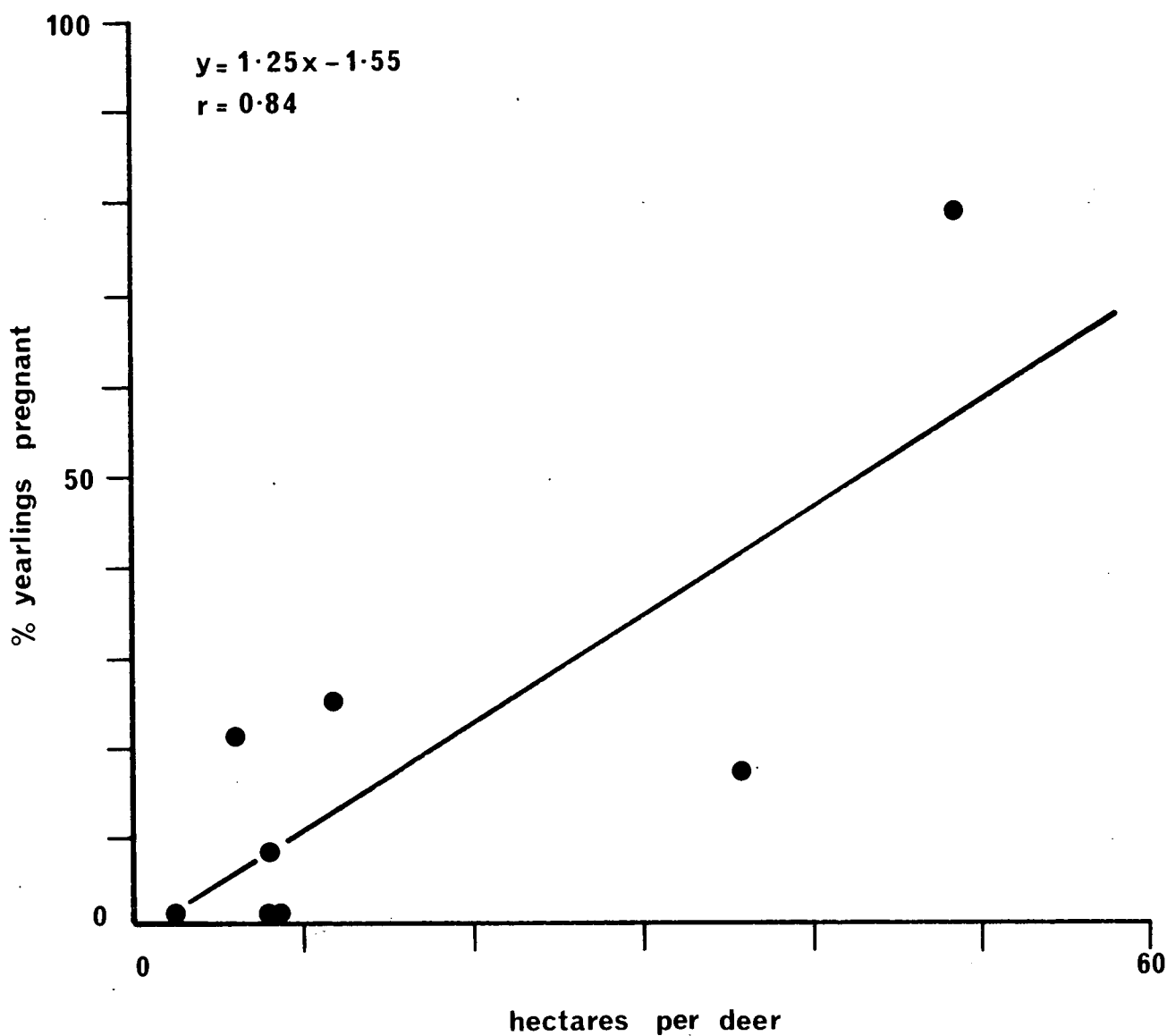


Fig. 4 Relationship between one aspect of performance (% yearling hinds pregnant) and an index of population density (ha per deer, i.e. 1/density). Data from eight different populations in Scotland.

be tested. From the information available we suggest tentatively that, where the overall deer density is 1 animal per 10 ha, tree establishment will occur if sapling numbers average, for example, 1/m² in 20% of the total area where the deer spend 50% of their time. Almost certainly the present extent of woodland would have to be increased to produce naturally such a sapling density. The work of Holloway and of Miller & Cummins described in 4.2.2 shows that the magnitudes are in the right order, but there are few opportunities for study at the critical threshold level for regeneration.

To sum up, the basic framework of the deer-habitat ecosystem in Scotland is confidently established. Reasonably precise estimates have been obtained for some of the quantities, particularly growth rates, population size and make-up, and life expectancy, and their range of variation is known approximately. But for many of the quantities relating to habitat selection, food

selection, home range, and the vegetation trends resulting from different amounts of usage, only approximate magnitudes can be suggested. A major problem baulking the development of a detailed predictive model is that measurements on the different factors have been obtained in different places; it is therefore unwise to relate them together until the effects of climatic, edaphic and topographic variables have been assessed. The greatest deficiency is, however, that the functional relationships between the component factors have not, in the main, been defined or estimated.

These difficulties, stemming from the number of factors and processes involved, apply to most attempts at modelling grazing systems, but, with red deer in the Scottish Highlands, there are additional problems caused by the terrain and the large size of the areas to be investigated. The alternative approach of studying

cause and effect by varying single parameters in series is probably even more demanding of research effort and facilities (Armstrong 1971). However, the strategy for research on red deer can profitably be influenced by a consideration of other research on grazing systems. Thus the work needed to gain an understanding of how the palatability and nutrient content of herbage affects intake, may be better done with other herbivores, and then extended to the deer. On the other hand, the relative lack of disturbance and management bestowed on the deer, and their ready visibility in moorland environments, may make them good subjects for research on dispersion and social organisation in ruminants. Another consideration applies: only some of the factors controlling the deer-habitat system can readily be manipulated by management. At present, the consequences of such manipulation, e.g. in soil nutrient status or shelter, cannot be reliably predicted. It may be expedient to seek such knowledge at an early stage in a research programme aimed at understanding the whole ecosystem.

The imperfect state of our present knowledge reflects the facts that systematic ecological research on red deer in Britain began relatively recently, and that input has been relatively small compared to the work on the main domesticated herbivores, and on cervids elsewhere in Europe and North America. The initial stimulus of British work on deer was the need for information on

population assessment and cropping (see Appendix); the greater concern now being shown in questions of impact should ensure that a more-complete understanding is obtained.

6.2 THE PROBLEMS POSED BY RED DEER IN SCOTLAND

Some of the management problems associated with red deer arise because their needs are not being met in present habitats, others are the inevitable consequences of the presence of a ruminant, because these animals have a relatively large intake and can utilise a wide range of plant material.

The marauding problem is largely in the former category, but can often be exacerbated by the juxtaposition of deer range and cultivated land. If sufficient shelter and good grazing were available in the normal range, the animals might be less induced to maraud. Whilst fencing can alleviate the problem, it is costly to erect, needs maintenance, and may not always be effective. The research need is to find the minimum provision of habitat factors required in the home range of the deer, and the relative strength of variations in these factors in influencing movements and home-range size. Further investigation is also desirable on the role supplementary feeding could play in controlling distribution.

The presence of red deer in woodlands is a rather

Table 11. The quantification of an apparently simple relationship: the determination of the deer densities compatible with tree establishment, showing component estimates, calculations and assumptions made.

Daily intake (dry weight) of average deer including calves	4 kg
Maximum amount of tree browse in diet over a year	25 %
Calculated maximum daily intake of tree browse over a year	1 kg
Weight (dry) of browse a deer would obtain from an average pine seedling	10 g
Calculated maximum no. of saplings that could be browsed by 1 deer in a year	36,500 saplings
Calculated maximum no. of saplings browsed per year by 0.1 deer/ha = 3,650/ha = 0.4/m ²	

On browsing, saplings are either killed or regrowth occurs; it is arbitrarily assumed that regeneration takes place if the numbers of saplings are such that the amount of browse available exceeds the amount the deer are able to take.

Any variation in the amount of browse taken per sapling in response to the numbers available, and in the sapling susceptibilities at different seasons, is ignored.

The area in which saplings occur will be less than the total range of the deer, and usage may be concentrated there. For areas of sapling occurrence of different extent and usage, the sapling densities resulting in regeneration at an overall stocking of 0.1 deer/ha are calculated as follows:

Extent (% of total area of deer range)	Usage (% of total deer time)	Resulting Deer Density (deer/ha)	Sapling Density per m ² giving Regeneration
50	50	0.10	0.4
50	80	0.16	0.6
20	10	0.05	0.2
20	50	0.25	0.9
20	80	0.40	1.5

These estimates need further modification because (1) the area that could support woodland will be less than the area in which seedlings occur, and (2) the deer will consume less than the maximum amount of browse when they frequent areas without seedlings as in summer.

different matter, because they are animals of the forest-edge and would occupy this habitat type by choice. Increasingly, plantations adjoin deer-forests, often being situated on ground formerly used by the deer, and it is almost inevitable that regular entry will occur. Sooner or later, permanent occupation will follow, because eradicating deer is extremely difficult from thicket-stage stands of conifers, especially when they are extensive, as in many recently established forests. Preparations should therefore be made now to deal with the problems that will arise. There is a precedent with roe deer, and like them, the red deer may become accepted as a sporting asset at densities compatible with tolerable amounts of damage; potentially, however, they are much more damaging. Research needs are of two sorts: firstly studies on impact to find out the likely amounts of damage and the reactions of the trees, so that vulnerable species can be avoided, and secondly investigations of ways of controlling damage. Knowledge on favoured food plants, and how far and how often deer will travel to obtain them, could be used to devise areas within forests attractive to deer, where they could be readily culled, or at least diverted from more-vulnerable areas. We can already advise on which trees are susceptible, but cannot predict how much damage particular deer densities cause; no other way of controlling damage than culling is practical. Even culling is difficult in plantations because we cannot predict deer movements or their usage of different areas with any certainty.

In natural or semi-natural woodlands in upland areas, red deer do damage more by preventing regeneration than by spoiling the timber, most such woodlands not being managed primarily for timber production. These woodlands have aesthetic value in enhancing landscape quality and providing a distinctive habitat for wildlife, besides giving shelter to the deer themselves. Research is needed to determine if natural regeneration will occur given deer densities and relative quantities of woodland that are realistic in deer-forests; if not, then to determine for how long it is necessary to prevent grazing to allow the establishment of trees. At present we can only speculate on these matters as in Table 11.

In typical, largely treeless, deer-forests the problems posed are perhaps not immediately obvious except in times of high deer mortality, but are nonetheless important because of the great extent of this type of habitat. Basically they concern 'carrying capacity' and animal yield: first, could the performance of the whole population, or of individuals, be raised by stocking at different rates and changing the management; secondly, are the present stocking rates causing changes in vegetation and soil, and, if there is decline in quality, is this decline irreversible. There is a third related question of whether the amount of secondary production harvested could be increased irrespective of changes in stocking rate by simply increasing or improving culling. To all these questions quantitative answers are needed, but cannot at present be given.

The research response could take the form of a series of monitoring projects on deer-forests where changes in culling rate, management type or stocking densities were made. This approach has already shown that greater yields of venison can be obtained by raising the culling rate. Similarly it might be shown that burning, by improving nutrition, raises individual performance, but it is important to find out how general and long-lasting are such effects. In some more-fertile deer-forests, nutritional demands may be satisfied in the absence of burning; in some deer-forests with harsh climates on infertile soils, the animal harvest may already be maximal. Only when an adequate description of the deer-habitat ecosystem has been obtained, with the quantities and functional relationships of the component factors defined, and their ranges of variation established, can these questions be answered with ease and precision.

Therefore, whilst accepting that red-deer performance is relatively poor in Scotland, we cannot judge whether high density or the basic poverty of the environment to which the deer are now restricted, is mainly responsible. Although present stocking rates in deer-forests have often been regarded as too great, there are several reasons for not excluding higher rates in considerations of optimising the use of such ground. On present evidence, the most serious consequence of deer presence is the prevention of woodland regeneration; this may well occur even at low densities. Above this level, impact may vary little, and indeed there is a suggestion from Rhum that reducing stocking rates to an intermediate level leads to unfavourable trends in moorland vegetation with respect to the deer. Also, present deer stocking is low in comparison to the densities of sheep in similar upland areas in Britain, and it may be increasingly acceptable to suffer poorer individual performance to obtain a greater yield from the population of red deer, especially at a time of world food shortage. Mixed-grazing systems involving cattle or sheep ought also to be considered. We would expect combinations of herbivores to make better use of the primary production, and there is circumstantial evidence (see 3.6.1) that red deer can benefit from the presence of other herbivores under British conditions.

Another system of pastoralism involving red deer is currently being explored, this being deer-farming, by which is meant the rearing of deer for meat production under management that is at least moderately intensive (see 2.4). Potentially, this could involve the control of pasture quality, with reseeded and paddock systems, the use of food concentrates and of health-maintenance measures, and also selective breeding for antlerless males, high twinning rates, calm disposition and high rates of food conversion. Solving the problems posed is more the role of agriculturalists and geneticists than ecologists, but there are no sharp dividing lines between high-input farming, low-input ranching and the traditional system of deer-forest management.

To decide which type or level of land-use is desirable needs information on all the alternatives, on what can be produced, on what they cost to set up and run in terms of manpower and materials, and on what effects they have on the habitat and neighbouring environments. It may be that poorer-quality land will be used for forestry, the production of plant fibre being the best way of utilising solar energy; it may be that recreational needs will be paramount. For these decisions, ecological facts are essential, even though at any one time they depend more on economic and political considerations. Therefore, a more-adequate understanding of the present and potential deer-habitat ecosystem must be obtained.

The research priorities that have emerged in the foregoing discussion are all associated with some aspect of the relationship between red deer and their habitat. A fundamental understanding is required of food selection and of dispersion patterns that would be equally relevant to traditional deer-forests, more-intensively managed grazings and woodland conditions. More-precise information is needed about the effects of habitat quality and population density on deer performance, and about the effects of the deer and associated management practices on vegetation and soil. Knowledge about impact in plantation woodland and on the regeneration of natural woodland is particularly desirable. There is also a need for comparisons between the major upland herbivores in performance and impact, and for evaluations of mixed-grazing systems and supplementary feeding.

6.3 SOME COMMENTS ON CURRENT MANAGEMENT

Although we did not intend to provide in this review a critique of red-deer management in Scotland, or a manual for management, nonetheless we are conscious that some of the facts now established are insufficiently applied or disseminated, and could with benefit be brought to general attention. Our aim is to stimulate deer managers to think more in ecological terms, redressing the emphasis of the popular hunting literature on technical matters such as rifle calibre, extraction and larding methods, with the hope that the biological basis of management can be optimised. Our main comments concern the management of deer on deer-forest land, but we would not wish to imply that such a land-use is the most appropriate; judgements on land-use are not based solely on ecological considerations and are outside the scope of this review.

We can be most definite with regard to cropping. Optimising output, either for sport or meat production, requires careful attention to the size and composition of the stock. If stags are the quarry, the population should contain equal numbers of adult stags and adult hinds, but, for meat production, a greater proportion of hinds is required. The objectives of the managers of deer-forests range between these extremes, but most often they want a high offtake of both products. In

consequence, there may be little advantage in trying to attain an equal sex-ratio of adult deer; a slight excess of hinds, as found in most populations, may suffice. In hinds, for either objective, there should be a predominance of the best breeders (3 to 8-year-olds). In stags, for sport, a high proportion of animals with maximum body weight and antler size (6 to 12-year-olds) is required, whereas, for venison production, a somewhat younger age-structure is better; the former age-structure is the most appropriate for present management. Achieving these age-structures means culling the poorer-quality animals in the younger and older age-classes, with most emphasis on young stags and older hinds. The animals to be culled should also include poor-looking hinds with poor-looking calves, late-born calves, since they usually die in winter, and 'knobbers' (yearling stags with small velvet-covered knobs rather than short unbranched antlers), since these are unlikely to develop into big adult stags. The tradition of avoiding calves and yearlings is mistaken since potential can be recognised most easily at these ages. Similarly, selecting hinds solely on their breeding status, as is common practice, is not so desirable as on their age and physical condition. Indeed, because of the late attainment of puberty and the prevalence of biennial conception, yeld hinds comprise the sexually immature, first breeders, and those adults most likely to be pregnant. Therefore, culling these animals leads to good-quality young stock being taken in mistake for older poor-breeders, reducing subsequent recruitment.

Efficient culling depends on an ability to assess the age and condition of both live and shot deer, and we must stress the need for stalkers to update their individual experience by comparing what is shot with their shooting intentions. The population diagrams used in deer-management in continental Europe provide useful guides for cropping and manipulating deer stocks. They are easily constructed from data obtained in deer counts, assuming an equal sex-ratio in calves, a maximum age of about 15 years, and an approximately pyramidal age-structure.

Until recently, Scottish red deer were undercropped, and the 'one-sixth-cull' recommended by the Red Deer Commission was a useful advance on the earlier practice of shooting a traditional set number of animals each year. Obviously, this rate may not apply equally to all populations, and, at best, a fixed rate can only damp down any natural fluctuations in a population. A more-satisfactory approach is to crop according to the recruitment rate, with adjustments to obtain desired changes in the size and composition of the stock. Regular counting is necessary, since a single count can be misleading, and it may be expedient to reassess the cropping rate every few years according to trends in the counts. The records in game-books should be reconsidered in relation to what is needed to monitor the consequences of management practices. Assessments of age, weight and condition, including the breeding status of hinds, are essential, and records should be

kept of natural mortality.

On habitat management, we would stress the desirability of maintaining a diversity of vegetation types, and increasing the extent of those types offering nutritious forage and shelter, although we cannot at present give precise estimates of the benefits conferred. The condition of the better grasslands should be given close attention, so that any adverse trends can be detected. Although red deer do not show such an intensive preference for *Agrostus-Festucetum* and related communities as sheep and cattle, these vegetation types are still highly preferred grazings, particularly in summer, and, unless they are of large extent, measures should be taken to reverse any tendency towards succession to dwarf-shrub heath. We would therefore qualify the view of Mutch *et al* (1976) that the presence of heavily utilised *Calluna* is a sign of over-grazing; only if such *Calluna* is widespread in the range of the deer and occurs on the poorer soils would we expect deer performance to suffer. A more-certain sign of over-grazing is the poor growth of grass on the greens amid a luxuriant bryophytic mat. To maintain the better grasslands, measures such as fertilisation, and the complementary grazing of cattle and sheep, should be considered where necessary.

Areas of scrub and woodland should also be carefully conserved for the browse and shelter they provide. Because the present ratio of herbivores to trees is so high, fencing will almost certainly be required at some period to ensure regeneration, but, thereafter, the areas can again be made available to grazing. The ideal for the future is to lower the mouth-to-tree ratio sufficiently to maintain regeneration with a minimum of fencing. As a step towards this objective, more-resistant species could be planted, with care taken not to create areas of good storm-shelter in places with preferred feeding, as this could cause heavy grazing before the hardest part of the winter and subsequently a concentration of animals in areas with no food. Less-palatable shrubs such as juniper might be useful, since they would be available late in winter both as food and shelter.

On burning, we would commend the code of practice produced by the Muirburn Working Party (1977). Very large fires should be avoided, so that a mosaic of age classes of heather can exist, providing both young nutritious growth and shelter over a wide area. Taller heather is particularly valuable to deer during heavy snowfall, and should be preserved, or allowed to develop, in a proportion of the low-lying ground used during periods of storm. We must warn, however, that the maintenance of dwarf-shrub heath at the expense of woodland through burning and grazing increases the rate of soil podsolisation, and although little further decline can occur in many poor soils, managers should be aware of the losses in fertility in better soils.

In making comments on supplementary feeding, we would again urge that the managers give regard to the biological implications of their actions, because there

are some strange anomalies in current practice. Although a main objective is to stop deer straying from the deer-forest, the young animals, which are more liable to move away, usually get little food and may not be so easily contained as the adults. Also, although feeding is aimed at improving the stock and decreasing mortality, it is curious that hinds are seldom fed and only some mature stags are given artificial food on most deer-forests. This implies a mistaken belief that better-fed males beget better offspring. Since these 'feeder' stags are seldom shot, we question why such animals should be winter-fed if they do not give benefit to the population or the estate revenues. Furthermore, the crowding that often occurs at feeding sites could easily create conditions suitable for parasite and disease transmission, besides doing local damage to the habitat. Nevertheless, with imaginative application, feeding could be developed into a more-useful management tool.

An important corollary of these comments on management is that deer should be managed in natural units. Deer are often not confined to one estate, and all or part of the stock may be shared at various times of the year by different owners. Hence deer can be subjected to different and conflicting policies. Co-operative management groups have already been formed in some parts of Scotland, but their success depends on a clear definition of management objectives and a total commitment to them. With such an arrangement, habitat improvements can be sited where most appropriate for the deer. It is also most desirable that the total stock be regularly counted and classified, and that the effectiveness of the policies adopted be monitored, with counts on natural mortality and adequate records on all animals culled. We would also commend the ear-tagging of calves, to obtain information on the movement patterns of the deer. A valuable discussion on the problems found in running such management groups is made by Mutch *et al* (1976).

The resolution of the problems of integrating deer-forests with other land-uses awaits a better understanding of subjects such as deer dispersion and home range, besides depending on economic, political and sociological considerations. However, it can be said with certainty that deer numbers compatible with deer-forest interests are not compatible with forestry, and sometimes also agriculture and conservation; therefore fencing is essential. Each situation has its own unique circumstances, and the management treatments adopted could well differ when deer cause damage in plantations immediately adjacent to deer-forests and when the damage is caused by deer emanating from afar. Within plantations, it is important to ensure that some food more attractive than the main timber trees is available, but care is needed not to create such favourable habitats that 'break-ins' from adjacent ground or high resident populations are encouraged. Either some preferred, but less valuable, trees should be

planted for browse, or some ground be left unplanted as feeding areas which would also help to make culling or counting easier.

Finally, we would draw attention to the fact that in many parts of the world e.g. continental Europe, North America and New Zealand, deer-management decisions are taken by groups which include trained wildlife biologists, often foresters. Regrettably the influence of

ecological thinking is much less formal and direct in Scotland. Whilst the experience and practical skills of Scottish deer stalkers cannot be discounted, there is no doubt that an inculcation of the underlying biological theories of wildlife management, both to the stalkers and those directing management, would enable better use to be made of what is a most important natural resource.

Appendix

HISTORICAL RÉSUMÉ OF NATURE CONSERVANCY INVOLVEMENT WITH RESEARCH ON RED DEER IN SCOTLAND

Foreword

In reviewing existing knowledge relevant to the management of red deer and their habitat in Scotland, we have adopted a biological classification of subject matter, and have taken a broad approach to the relevant world literature. This has obscured the course and achievements of some twenty years of Nature Conservancy effort centred on red-deer management in Scotland. This supplement describes how it arose, who was involved and where the research was done.

Early involvement by the Nature Conservancy

When the Nature Conservancy was set up in 1949, there was widespread concern about the status and management of red deer. Although popularly referred to as 'the red-deer problem', it was, in fact, a complex series of problems. Public concern was greatest about poaching (i.e. killing deer on other people's land) which had developed on a commercial scale in parts of the Highlands. Public opinion was inflamed on account of the cruelty involved; the killing was often done with unsuitable weapons, in haste, in twilight or darkness, and with little regard to any wounded animals. The law in Scotland had little power to deal with unauthorised deer-killing since there were no statutory close seasons, and the penalties were insignificant compared with the market value of deer carcasses. Moreover, many areas where large concentrations of deer occurred were close to roads, and they were difficult to keep under surveillance.

However, there were deeper problems of management, less widely appreciated, but with a longer history, involving various land users directly concerned with red deer in Scotland. Deer-forest proprietors were worried about the declining quality of Scottish red deer, about poaching and about the fate of deer which wintered away from the deer-forest land; farmers, foresters and other land users were concerned about the effects of seasonal 'marauding' or permanent 'colonisation' by red deer. Deer fences were expensive and not always deer-proof. There was no legal requirement for deer-forest proprietors to fence in the deer or to pay compensation for deer damage, and it was generally too expensive for the smaller farmers and crofters to fence their crops of turnips and autumn-sown cereals, or to prevent grazing competition by deer. Deer-forest boundaries seldom enclosed natural deer population-units, and there was little co-operative management. There was no tradition of counting deer, owners were not obliged to disclose their shooting figures, and stocks were underexploited for fear of population depletion. Since hinds had little commercial value they were either unshot or only lightly exploited. So, although there was some evidence of undercropping, detailed information was lacking.

These problems, recognised for over 100 years, had be-

come increasingly important due to the mounting demands for hill-land for agriculture, forestry and other purposes. Pressure on the lower land had resulted in a decrease in the amount of winter grazing available to red deer, but the extensive areas of summer grazing were little affected. Between 1872 and 1954 aspects of the deer problem had been considered by eight different governmental enquiries and investigations, but with little real effect. The last two enquiries, the Committee on Cruelty to Wild Animals (known as the Scott Henderson Committee), 1949-51, and the Committee on Close Seasons for Deer in Scotland (known as the Maconochie Committee), 1952-54, stimulated interest in the Scottish situation. Recommendations of the Scott Henderson Committee led to the introduction of a Deer Poaching (Scotland) Bill, which failed after its third reading in the House of Lords.

The Nature Conservancy, with its responsibility for advising on the conservation and control of flora and fauna, soon became involved with red deer. Dr. Fraser Darling was contracted for six years from October 1952 to undertake a Red Deer Survey to obtain factual information about Scottish red-deer populations. A confidential report on the preliminary results was submitted to the Conservancy in 1955. Also, discussions in 1955 with the four organisations principally involved with red deer in Scotland (i.e. the Scottish Landowners' Federation, the British Field Sports Society (Scotland), the National Farmers' Union of Scotland, and the Blackface Sheep Breeders' Association) resulted in a joint report being submitted in 1956 to the Secretary of State for Scotland. This led to the Deer (Scotland) Act 1959. Its provisions included close seasons for red deer (from 1962), other anti-poaching measures, and the setting-up of the Red Deer Commission with advisory responsibilities and special powers to deal with red-deer problems.

The Red Deer Survey (1952-1958)

Darling's objectives were to gather data on the distribution, abundance, population composition and cropping of Scottish red deer. Two professional deer stalkers were recruited in early 1953 for seasonal counting work. A complete count over the total area occupied by red deer was impractical and sample areas amounting to 25-30% of the known deer range were selected. The counting method was not tested during this survey, but care was taken to prevent double counting; it was assumed that the counts would under-represent the deer actually present.

Many owners requested that the results should not be released on an individual estate basis, and the detailed results were never published. The Annual Report of the Nature Conservancy for 1960 mentioned that over 52,000 deer (16,000 stags, 26,000 hinds and 10,000 calves) were counted on some 662,000 ha of deer ground (455,000 ha of recognised deer-forest and 207,000 ha of marginal land).

The survey also confirmed that shooting pressure was low compared with post-winter recruitment. In rough terms, the average post-winter calf survival rate was 34-38 calves/100 hinds, and the shooting pressure was equivalent to only about half this rate, with about twice as many stags as hinds being shot annually. Most large blocks of deer ground had more hinds than stags, as might be expected.

The Red Deer Commission

The Red Deer Commission was set up under the Deer (Scotland) Act 1959, comprising a chairman and twelve other members representing the interests of nature conservation (2), owners of land used for agriculture or forestry (3), sport (2), farmers and crofters (3), and of hill-sheep farmers (2), together with administrative and field staff. Apart from investigating complaints of marauding deer and dealing with deer control, the Commission recognised the need for co-operative management over natural deer-population units. The latter had to be defined arbitrarily from practical experience of what natural or man-made features represented reasonable barriers to deer movement. It was thus necessary to count the deer over large tracts of country, and to work out overall rates of cropping to be shared out amongst the various properties contained in each unit. Estates also were encouraged to organise their own deer counts, but until recently there was little evidence that many of them did.

Much of Scotland's total red-deer ground has now been covered at least once since 1960 by the Commission's counting team, giving a useful overview of the total population, its composition and changes. In recent years, the annual counting programme has included at least one large area of previously uncounted ground, and recounts of some areas done earlier to check population trends. Whilst the earliest counts indicated a total population of around 200,000 red deer, the most recent data suggest that this has increased to about 270,000.

The Nature Conservancy received contributions from the Commission towards research costs up to 1966, and advised the Commission on cropping rates, whilst Conservancy stalkers assisted in the Commission's annual deer counts. The Commission undertook the counts on Rhum from 1966, and all those at Glen Feshie in support of the Conservancy's research programme (1967-73). The Conservancy marked deer calves at Glen Feshie, as did the Commission on surrounding areas from 1967, to provide data on movement of deer within this large area. The Commission's deer control work also provided useful research material.

The Commission initiated The Deer (Amendment) (Scotland) Act 1967 and The Sale of Venison (Scotland) Act 1968. The first makes it possible to sample red deer for scientific purposes in the close season, and the second provides essential data on current cropping levels.

Studies on the Island of Rhum (1957-1966)

Acquisition of Rhum as a National Nature Reserve by the Nature Conservancy in 1957 gave new research opportunities with regard to red deer. This 10,600 ha island then carried about 1,500 red deer, 2,000 hill sheep and 50 hill cattle. There was also a small population of feral goats and a herd of ponies.

The first priority in the Management Plan was to redress the supposed ill-effects of the previous grazing and burning regime (Eggeling 1964). Restoration of woodland cover, cessation of burning, and reduction of grazing were higher priorities than research. Deer research was visualised initially in this broad conservation context, but Rhum appeared the ideal test-bed for population studies.

In 1958, burning was stopped, sheep and cattle were removed, and the deer cull was arbitrarily increased from 40 stags and 40 hinds annually (roughly 30% of the recruitment rate as measured in 1957) to 100 stags and 140 hinds annually. The cull was made as evenly as possible over the island. This new rate of cropping, which amounted to about one sixth of the adult stags and hinds as counted in spring, did not, in fact, reduce the population and it was decided to continue this treatment to confirm the results.

From 1957 to 1966, the deer population on Rhum was studied by V.P.W. Lowe, with annual counts of the live population in early spring and searches throughout the year to find natural deaths. The main objectives were to check the accuracy of the deer-counting method, to describe the responses of the population to the culling treatment, and to describe the properties of the population in terms of growth, reproduction and longevity. The results of this work gave the Red Deer Commission quantitative data on which to advise landowners, and they adopted the 'one-sixth cull' as a useful starting point for deer culling at a local level.

Subsidiary work included marking calves to provide known-age material for studies of age estimation, to study deer movements, and to obtain life-table data from unshot deer. The latter objective proved impractical due to the losses of ear-tags from the deer. R.W. Youngson assisted from 1964 in studying aspects of dispersal and home-range behaviour since these processes were relevant to colonisation and marauding. These studies were stopped in favour of other research projects.

Whilst Lowe's work was concerned largely with the properties of the red-deer population, the need for studies on their interactions with habitat was also appreciated. Two other research projects on Rhum were related to this latter objective: mapping the island's vegetation by R.E.C. Ferreira (1961-1964), and studies of the vegetation used by the deer in one part of the island by W.N. Charles, D. McCowan and K. East (1963-1965). Ferreira's mapping project had also to satisfy conservation requirements; nevertheless, it

provided a meaningful vegetation classification, and useful material for the work by Charles, McCowan and East. In addition, plots were set up in 1958 by D.A. Ratcliffe to determine floristic changes in selected vegetation types associated with the new management regime. These plots were subsequently examined by M.E. Ball in 1970.

Whilst these projects on Rhum yielded a great deal of useful data (discussed elsewhere in this review), there were some problems of interpreting trends in the deer and in the vegetation. These arose mainly because so many management changes were made simultaneously soon after take-over. Contrary to earlier expectations of improved deer performance due to reduced grazing competition, Lowe found slight downward trends in some aspects of performance. He attributed these to changes in the nutritional status of the vegetation, the hypothesis being that the deer were unable to maintain the vegetation in the same favourable state, but there were no quantitative measurements or controls. Some vegetation changes were later confirmed by Ball (1974). Moreover, work by Miles (1971) showed that *Molinia*-dominated vegetation, of which there is a great deal on the island, was markedly more attractive to red deer for about two months immediately after burning in the spring. Although the trends in animal performance were associated with vegetation trends, it was not possible to isolate causes.

Other problems of interpretation arose with the population data collected after 1965 (unpublished). Up to 1965, slightly more deer were counted than expected in most years, but later counts up to 1976 mostly showed fewer deer than expected and the discrepancies were larger, the largest being an apparent loss of 270 deer over a two-year period. This change in the consistency of results coincided with changes in methodology. Due to the needs of other research projects, effort was reduced in monitoring the Rhum population and the natural-mortality searches were not so intensive as before. Also, from 1966 the counts were done by the Red Deer Commission's field staff, but two years were missed. This larger team counted the island in a shorter time (1-2 days) than previously (c. 5 days), and portable radios were used to reduce possible errors due to deer movements and double counting. These counts were potentially more effective than the earlier ones, although there was no evidence that the first counts were inaccurate; indeed the population reconstructions made later suggested a high degree of accuracy in the earlier counts. Also, there were no indications of exceptionally high natural mortalities in the years after 1965. Thus, changes in methodology did not provide a satisfactory explanation for the discrepancies. Other possibilities included the voluntary emigration of deer and increased poaching. There was some evidence of poaching from boats and the greatest apparent losses coincided with high venison prices, but

poaching on such a scale seemed unlikely on Rhum. Alternatively, changes in vegetation might have led to greater numbers of deer frequenting the steep coastal grasslands and the shore; if any died there, carcasses could be washed away and not found. However, natural mortality would have had to be considerably higher than before to support this hypothesis.

Since none of these factors can be quantified, the situation is unresolved. The desirability of further investigation is highly debatable because of the large research input needed, amounting to a repeat of Lowe's study with extra emphasis on natural mortality and other factors likely to cause losses. Also, if poaching or events special to the period of the discrepancies were to blame, nothing would be found; the study would only be worthwhile if an unexplained trend in numbers were still occurring.

In addition to the Conservancy's own research, two other deer-research programmes undertaken on Rhum should be mentioned here. A group from Cambridge led by R.V. Short and including G.A. Lincoln, Fiona Guinness and T.J. Fletcher worked on aspects of reproductive physiology and associated behaviour from 1967 to 1973. T. Clutton-Brock (Cambridge University) and Miss Guinness are currently working on dispersion and evolutionary aspects of red-deer social behaviour.

Mainland research (1959-1966)

It was important to find whether red deer elsewhere on Scottish hill-land showed similar population properties to those on Rhum, and work was started on mainland areas by B. Mitchell in 1959. On privately-owned land, experimental alterations of the traditional culling practices were impractical. Thus, deer counts and mortality data were used to compare post-winter recruitment rates, and animal performance was studied using the deer shot normally for management purposes. Studying performance meant first developing methods of post-mortem age estimation, and useful methods resulted from the studies on Rhum by Lowe and those on the mainland by Mitchell.

Research material was collected by the Red Deer Commission, mainly from marauding deer and partial shoot-outs, but the main work was concentrated on two deer-forests differing in vegetation and climate from Rhum: Glen Fiddich (Banffshire) and Invermark (Angus). Glen Fiddich had a lower population density (740 deer on 9,242 ha) than Rhum and it was enclosed by a deer fence during the study period (1961-1965). Invermark had a slightly higher population density (1,850 deer on 12,140 ha) and was not isolated by deer fencing. Both areas were predominantly heather-covered and had more continental climates than Rhum. Post-winter recruitment was shown to be remarkably similar to that on Rhum, but other aspects of performance were more variable. It was not possible to explain this variation, emphasising the need for much larger surveys with more-detailed environmental assessments

to produce a general understanding of population dynamics and performance in red deer in the Scottish uplands.

Range Ecology Research (1968-1973)

Habitat Teams were formed in the Nature Conservancy in 1966 to plan conservation-research requirements on a habitat basis. Within the Mountains and Moorlands Habitat Team, I.A. Nicholson developed a Range Ecology Research Group (in 1968) from botanists and deer-research staff in Scotland. The main purpose of this group (*Range Ecology Research : Research Programme & Planning Papers*, mimeographed report, Nature Conservancy, Edinburgh 1969) was "to encourage closer team work and to create a unit able to handle a broad spectrum of ecological problems in the mountain and moorland habitat . . . bearing in mind the need to understand the principles and processes in mountain and moorland ecology as a basis for management . . .". Deer-habitat interactions were accepted as one of the key focal points for the attention of this group. Botanical work included the effects of deer and other large grazing mammals on vegetation dynamics and succession. Three main, though not mutually exclusive, aspects of zoological work were identified for study: (1) population dynamics and performance; (2) factors affecting dispersion; and (3) nutrition i.e. nutritional requirements of the deer and how these are met in existing habitats.

B.W. Staines who had previously studied the ecology and management of red deer in Glen Dye, Kincardineshire, began work on dispersion, particularly the segregation of stags and hinds. Pamela Arman was recruited as a nutritionist, and worked initially at the Rowett Research Institute on lactation and early growth under different nutritional regimes. Other red-deer studies planned as parts of the Range Ecology research programme included a study of the annual cycles of condition and body composition of selected classes of red deer done by B. Mitchell on Rhum. This work was designed to investigate aspects of growth in wild red deer giving data relevant to the development of nutritional studies of deer in the field.

The formation of the Range Ecology Group coincided with the establishment of a new relationship between Glen Feshie Estate (a 16,600 ha deer-forest in the Cairngorms) and the Nature Conservancy. The eastern part of Glen Feshie was already under a Nature Reserve Agreement made with the previous owner. The new owner invited the Nature Conservancy to advise on management and offered research facilities on the area. Investigations on the properties and responses to management of the red-deer population had been started by B. Mitchell in 1966 and this was expanded later as part

of the Range Ecology research programme. Glen Feshie was therefore regarded as a research and development area where management problems relevant to a substantial part of Highland Scotland could be investigated. The work comprised:

- (1) Short-term studies to enable the Range Ecology Group to advise on the management and development of the estate;
- (2) Monitoring the deer population and its range to evaluate the effects of the development plan based on Nature Conservancy recommendations and the estate's own objectives;
- (3) Basic research on aspects of the interactions between deer and their range.

The overall development plan drawn up was not designed to test the relative effect of individual treatments, and the monitoring exercise is unlikely to be completed, its value having fallen because the recommendations were not all implemented. In particular, the deer cull was to have been increased to reduce the hind stock, but this, which gave the monitoring exercise much of its value, was not accomplished.

Botanical work in several study areas on the interactions between red deer and their range (see Nicholson 1970) included the following:

- (a) The effects of management, including burning, on the attractiveness to red deer of vegetation dominated by *Molinia caerulea* (J. Miles);
- (b) The effects of various herbivores, including red deer, on upland vegetation types (D Welch);
- (c) The effects of grazing and browsing on the regeneration of shrubs and trees, and on the growth and survival of saplings (G.R. Miller);
- (d) A survey of damage by red deer in planted woodlands (C.O. Badenoch, I.A. Nicholson & G.R. Miller).

It was planned to bring together much of the Range Ecology Group work in the form of a systems model of red-deer range using Glen Feshie as an example, but due to redeployment this was not completed.

In 1973, with the formation of the Institute of Terrestrial Ecology and the consequent changes in research structure and policy, the Range Ecology Group was disbanded. Some of the allied botanical projects are continuing towards completion, and the zoological projects on deer are currently being written-up. These first Range Ecology Group projects were regarded as steps towards the development of a more-integrated approach to herbivore-range interactions, but the break-up of this multidisciplinary research group after only five years means that these aspirations remain unfulfilled. However, the important research priorities were, we feel, correctly identified, and work in these fields is still much needed.

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Red deer are becoming increasingly important in upland Britain, not only as sources of food, pleasure and sport, but also because of the damage they cause to farmland and forest. This book provides a much-needed review of the extensive scientific and popular literature on red deer, and will be of interest to the professional and layman alike. It gives a fascinating account of the ecology of Britain's largest land mammal, highlights the important gaps in our knowledge, and suggests how the recently acquired information can be usefully applied in present-day management.

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